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BIOLOGICAL HIGHWAYS IN THE SKY

The dispersal of microorganisms, insects and other small life forms via the atmosphere

Cindy E. Morris, Leda N. Kobziar, Brent C. Christner, Claire Garros, François De Vleeschouwer, eds

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Introduction

The precarious yet never-ending cycle of voyages on high

Cindy E. Morris, Leda N. Kobziar, Brent C. Christner, Claire Garros, François De Vleeschouwer

⏩ Highways on high, bustling with minute creatures, come into view

Earth's troposphere is characterized by large-scale movement of air masses that transport moisture and particles from natural and anthropogenic sources at scales of a few meters to thousands of kilometers. Particulate matter moved by air masses can be inert or of biological origin. Dust storms and volcanic eruptions can liberate massive quantities of both types of particles thereby making their flight pathways visible. Likewise, pollen is the most prominent and intensively studied of the biological particles due to predictable times of flowering of different plant species and the resulting downwind allergy seasons. Nevertheless, air masses also transport tons of viable cells, spores or fragments of microorganisms as well as small arthropods. These organisms can ride the winds passively –for at least a part of the voyage– and much more surreptitiously than inert particles and pollen. Overall, the aerial dispersal of biological particles is of considerable importance for the health of animals, humans and plants and plays a role in the ecology and evolution of the organisms thus disseminated –whether we are aware or not of these movements. Many of the consequences of large or even local-scale aerial transport of microorganisms on the biogeography of Earth's flora and fauna and on a range of environmental processes are yet to be determined. Most apparently, the consequences of large-scale atmospheric movement of microorganisms manifests itself, for example, in disease emergences in new regions. These include the outbreaks of coffee rust in Brazil in 1966, of soybean rust that spread from Asia to Africa to South America and then to North America in the early 2000's, and of foot and mouth virus in pig farms in the UK in 1981 (Morris and Martinetti, 2023). In the same vein, the long-distance aerial movement of spiders by ballooning contributes to connectivity and gene flow among their populations as observed among the hundreds of spider species on the Iberian peninsula, for example (Domènech *et al.*, 2022). Mosquitos that harbor arboviruses, protozoans, and helminths affecting vertebrates and humans pass at high altitudes over West Africa thereby re-seeding epidemics and confounding ground-based efforts at control of diseases carried by this vector (Bamou *et al.*, 2024).

Air masses also uplift a wide diversity of metabolically active microorganisms into clouds (Amato *et al.*, 2017) where those with special traits –such as the highly active ice nucleating proteins on their surfaces– can trigger the freezing of cloud droplets leading to the formation of snow and rain (Morris *et al.*, 2014b; Stopelli *et al.*, 2017).

The principles of aerobiology were established in the early 1900's mostly from the efforts of plant pathologists who sought to understand and manage disease spread (Gregory, 1961; Stakman and Christensen, 1946; Stakman *et al.*, 1923; Wolf, 1943). Their knowledge of the atmosphere as a vector for microorganisms was founded, in part, on previous inventories of living microorganisms in the air documented in the late 1800's by naturalists such as C.R. Darwin (1846) or by a microscopist at the meteorological and astronomical observatory in the Montsouris Park in Paris (Miguel, 1883). The struggle to understand the spread of stem rust of wheat, as the cultivation of this staple crop expanded from Mexico to Canada in the early 1900's, led to the discovery of an aerial "Puccinia Pathway" over the Great Plains of North America where spores of the fungus *Puccinia graminis* moved successively northward at several kilometers altitude according to the cropping calendar (Aylor, 2003). Similar trajectories of long-distance dissemination have since been revealed for the spores of the oomycete that causes Blue Mold of tobacco (Aylor, 2003) and for stem rust of wheat across China, across South America and across Western Europe-Maghreb (Radici *et al.*, 2022). Nevertheless, in spite of the precocity of some of these achievements, few details are known about the aerial movements of most of the biological particles that travel on the highways of the atmosphere. Discovery of the aerial trajectories of the rust fungi and oomycetes mentioned above was greatly facilitated by the host specific nature of these obligate parasites whereby the location of sources and sinks can be readily determined. However, many of the biological particles in the atmosphere can dwell in a multitude of diverse habitats making it very difficult to specify the most likely sources or the timing of release into the atmosphere. Therefore, at present, the movement of most biological particles via the atmosphere can only –at best– be deduced from ground-based observations.

⏩ A book to sharpen our perception of the atmospheric highways

The objective of this book is to bring to center stage the current knowledge about voyages of small biological particles in the atmosphere, with a focus on microorganisms and small insects but applicable to nematodes, spiders, tardigrades, etc., referred to hereafter as microbial particles. Research in aerobiology has contributed to the current image of an atmosphere teaming with so much biology (Després *et al.*, 2012; Fröhlich-Nowoisky *et al.*, 2016) that one wonders to what extent it is a *bona fide* ecosystem compared to its role as a means of transport (Lappan *et al.*, 2024). The challenge to addressing this question lies in the difficulty of describing the spatial and temporal dynamics of the microbial particles in the atmosphere compared to describing traits and structures of groups of microbial particles that represent snapshots of these dynamics. As early as 1944, scientists who were responsible for plant quarantine services professed the importance of elucidating these dynamics because it could help to anticipate the arrival of plant pathogens into new regions via aerial dissemination (Mccubbin, 1944). However, today there have still not been attempts to

estimate the risk of arrival of new pathogens via natural atmospheric dispersal relative to the risks engendered by transport of commercial goods or passengers. By compiling current knowledge about the long-distance voyages of microbial particles, about the status and perspectives for analytical tools, and about applications of such knowledge, we hope to offer stimulus to both new and established researchers to undertake an important challenge in aerobiology. This challenge is to more precisely characterize and quantify the dynamics of microbial voyages on the highways of the atmosphere and identify the impacts of these voyages on disease epidemiology, environmental quality and the evolution of organisms.

The long-distance dispersal of microbial particles via the atmosphere and their incursion into new geographic regions involves three basic steps: i) emission of particles into the atmosphere from a source such that they escape the boundary layer and enter the free troposphere, ii) transport in the free troposphere via the movement of air masses and iii) deposition out of the free troposphere (Morris *et al.*, 2014a). The intensity and characteristics of each of these steps, and their consequences on the environment and the fate of the microorganisms and arthropods and other microbial particles thus transported, depend on an interplay of physics, chemistry and biology. The sections and chapters of this book provide a conceptual foundation and framework to analyze each of these steps from the perspectives of physics, chemistry and biology and highlight the tools and concepts needed to conceive the probable aerial trajectories, to validate them and to understand their implications for animals, humans and the environment.

⏩ The physics of the voyage – Section 1

The first section of the book (Chapters 1 to 4) addresses the physical nature of atmospheric highways and the capacity of microbial particles to be transported by them, thereby providing insight into the principles needed to understand how biological particles access and ride the atmospheric highways. This includes a description of the major movements of air masses, of the physical traits of microbial particles that define their aerodynamics, and an overview of the methods for quantifying the dynamics of flux of microbial particles into the atmosphere.

Chapter 1 provides a concise and comprehensive presentation of Earth's different patterns of air mass movement at present, in the past, and what can be anticipated in the future in light of climate change. Much of our understanding of particle transport by these air mass movements comes from the study of dust dispersal. The similarity of aerodynamic properties between some dust particles and microbial particles makes it possible to speculate on the capacity of these air masses to transport the latter, as further explained in Chapter 4.

Chapter 2, as its title specifies, is a primer on the aerodynamics of microbial particles. This chapter presents, in simple terms, some of the physics of small particles that underlie their ability to float and to seemingly defy gravity. It also presents a compilation of the data that have been published over the past 100 years on direct measurements of aerodynamic traits –such as terminal velocity and aerodynamic diameter– for small particles in the size range of microorganisms and pollen. These aerodynamic traits are of major importance for determining the capacity and duration

of flight for given atmospheric conditions. This chapter addresses the critical point that physical diameter is not always a good predictor of these traits and illustrates examples of deviation. This highlights the importance of making direct measurements of aerodynamic traits such as terminal velocity or aerodynamic diameter to validate estimates based on physical dimensions, especially when the shape of the microbial particles deviates markedly from spherical –as is the case for many fungi in particular. The chapter illustrates the consequences that errors in estimation of aerodynamic dimensions can have on simulations of the extent and trajectory of aerial dispersal.

Chapter 3 marks the beginning of the adventure into the atmosphere. This chapter addresses the question of how we can measure the rate of emission of microbial particles, i.e. flux, into the atmosphere. Obtaining direct measurements of flux of microbial particles into the atmosphere has been a major technical challenge in aerobiology. In the 1980's and 1990's, the teams of B. Lighthart (1994) at the US Environmental Protection Agency in Corvallis, Oregon and of J. Lindeman (1982) at the University of Wisconsin-Madison Plant Pathology Department measured flux with field set-ups that involved multiple heights for microbial sampling on towers equipped with probes measuring wind speed gradients. This allowed them to report site-specific values of net upward movement of particles per m^2 per second and its diurnal cycle. However, after these herculean efforts, there have been few other attempts at direct measurement. Interest in flux of microorganisms was renewed about 15 years later when the teams of S. Burrows (2009b) and A. Sesartic (2011) used modeling to estimate global flux rates based on the abundant data for microbial concentrations at single heights above the ground across a wide range of geographic sites and habitats. Their flux estimates attributed mean values of fluxes to each of a dozen or fewer biomes over large geographic regions depending on the general type of land cover. However, without validation that the concentrations are proxies for flux, there is much uncertainty in these estimates. As Chapter 3 points out, the multitude of assumptions used in this approach to estimating fluxes leads to large uncertainties ranging up to nearly 1000% of the estimated values. Uncertainties could be reduced with ground-truthing of source strength that includes concentration measurements not only at the source site but downwind as well (Aylor, 2017; Aylor *et al.*, 2011). The ideal goal is to quantify fluxes for specific sites, at specific dates and for specific microorganisms that have impacts on the health of humans, animals or plants or on cloud processes, and to understand how source strength influences emissions.

Once microbial particles are emitted into the atmosphere, it is unlikely that we will be able to observe directly their flight paths as vividly or distinctly as for dust, volcanic ash or fire plumes. In this light, transport models are of great importance for prospecting the trajectories and fates of microbial particles in the atmosphere and their eventual deposition. Chapter 4 presents the fundamentals of these transport models. Although these models have been developed and validated mostly from research on the transport of dust, Chapter 4 points out their utility for microbial particles. The validity of transposing knowledge obtained for inert particles to microbial particles is based on the physics that underlie these models and the strong influence that aerodynamic properties of particles have on flight –whether they are inert or of biological origin. Whereas some of these properties were presented in Chapter 2 in rather simple form, Chapter 4 provides more precision and mathematical formalism all while keeping the subject accessible to biologists.

⏩ Postcards from tiny travelers – Section 2

The second section of the book (Chapters 5 to 10) is a compilation of what might be considered the travel diaries of insects and microorganisms that ride the winds. In the same way that postcards are meant to appeal to our curiosity about the climate and scenery experienced by friends and family during their travels, this section begins with two chapters on the environmental conditions that microbial particles experience in the atmosphere. During their atmospheric voyage, microbial particles are either in dry air (absence of condensed liquid water) or inside water droplets (liquid or frozen). Chapter 5 is a *tour de force* of the open-air factors that can stress, age, corrode or perhaps stimulate biological particles in the atmosphere while they are outside of water droplets. The atmosphere is indeed an extremely harsh environment. The survival of microorganisms and insects under these conditions is a testament to the multitude and robustness of traits for resisting ultraviolet radiation, drying conditions, chemical radicals, and electrostatic fields, for example. This robustness might reflect the evolutionary history of microorganisms that started before the existence of all other life forms. Microorganisms began to colonize land from the oceans during the Early to Middle Precambrian era about 1,800 to 2,750 million years ago when they were the only forms of life on Earth and the continents were barren and hostile. After initial excursions into the atmosphere from sea spray, they adapted to the more efficient land-to-air uplifting and dispersed inland via winds (Henderson and Salem, 2016). This was a test of their aptitude for life in the air and the beginning of epochs of opportunity to reinforce these aptitudes.

Chapter 6 presents the perspective of air-borne microbial particles from within water droplets –based on research on real or simulated cloud droplets and bulk cloud water. The presence of free water obviously opens up the question about metabolism of the chemicals diluted in atmospheric water droplets. This chapter points out that the remarkable difference between metabolic profiles of microorganisms in dry air vs. water droplets is that the former show signs of DNA damage and oxidative stress whereas the latter seem to reveal the expression of genes involved in central metabolic pathways, production of ATP, consumption of carbon and transmembrane transport of various compounds. Indeed, microorganisms in atmospheric water droplets are tasting the local cuisine. Furthermore, within water drops in the atmosphere, fungi can also initiate germination. Nevertheless, this chapter clearly exhorts that, in spite of the capacity for microorganisms to produce biomass in cloud droplets, the rate of production under cloud conditions is too slow relative to the short life span of droplets. This makes it very unlikely that there is microbial multiplication in the atmosphere. This will lead the reader to wonder if an environment that cannot support multiplication of its occupants can be considered a habitat. This strengthens the argument that the atmosphere is mostly a transport system with roadways, service stations, and exit ramps.

The microbial particles emitted from land surfaces by turbulent and convective movement of the air have received the most attention in aerobiology (Burrows *et al.*, 2009a; Després *et al.*, 2012; Morris *et al.*, 2014a). Therefore, in this book, we have chosen to highlight the voyages of microbial particles emitted from sources and via mechanisms that are less often in the forefront and that are emerging subjects of research. Chapters 7 and 8 present the emissions and transport of microbial particles from two contrasting mechanisms: via bubble-bursting from surface waters –ocean waters, fresh

waters and waste waters– (Chapter 7) and via wildland fires (Chapter 8). The respective fields of study have been named ocean aerobiology and pyroaerobiology. Although surface waters and terrestrial habitats are quite different in terms of their reservoirs of microbial taxa that can become aerosolized, studies of emissions from these two sources reveal that enrichment processes for certain taxa are active for both of these distinct reservoirs. For waterborne microorganisms, enrichment from the surface to aerosols favors hydrophilic organisms. This enrichment is further enhanced by the formation of microlayers on ocean surfaces that concentrate organic material and certain microorganisms and microbial assemblages (Cunliffe *et al.*, 2013). Therefore, the diversity of biological particles emitted as aerosols from seawater are enriched from a pool that, itself, is not fully representative of those in the bulk seawater community. In spite of the multiple levels of enrichment from bulk water to aerosols, the study of emissions of biological particles from water surfaces has been facilitated by experimental set-ups that simulate emissions. This has led to progress in understanding the importance of water temperature, salinity and droplet size, for example, in emission rates and transport of particles in the atmosphere.

Chapter 8 describes the surprising phenomenon of emission of viable microbial particles during fires. Plumes of smoke from major fires are visible from space and make long journeys, crossing continents and oceans. These plumes transport up to 85 Tg of particulate matter annually whose composition has been well documented in terms of its highly oxidized organic materials, incomplete combustion products, and various minerals. However, it was recognized only recently that smoke has the capacity to transport viable microorganisms (Kobziar *et al.*, 2018). Furthermore, these viable microorganisms seem to be released into the atmosphere during the burning process itself and they somehow survive the heat of the fire. Even more surprisingly, smoke generates greater concentrations and diversities of bacteria and fungi closer to the source of the fire than farther away. This reflects a broadly established truth about fire that may seem counterintuitive but is well known among fire ecologists: that wildfires appear destructive but their ecological effects are complex and nearly always include a high degree of spatial variability from severe to benign to beneficial impacts (Kobziar *et al.*, 2024); This discovery provides an excellent basis for direct observation of dispersal pathways of microbial particles and will likely open investigation into what other types of small organisms can ride smoke plumes.

Chapter 9 gives voice to another biological passenger on the atmospheric highways that is rarely included in discussion of atmospheric microbial particles: insects. Even winged insects can depend on passive dispersal by winds for part of their long-distance dissemination. Their biology, aerodynamic properties, and strategic deployment or retraction of wings are adapted to this means of dispersal. In addition, for many insects, knowledge of their dispersal or migratory pathways is based on data from a few traps and various indirect observations, leading to the inference of their dispersal trajectories in the same manner as they are inferred for microorganisms. This chapter presents an inventory of the insects that travel via air mass movement and raises the issue of the passive component of dispersal. Similar inventories could eventually be made for nematodes, spiders and tardigrades, for example, when sufficient data become available. Although part of the dissemination of insects is passive, they can use celestial clues and Earth's magnetic fields, for example, to trigger active take-off and descent. Perhaps this is analogous to active release of spores of certain

fungi as part of their emissions strategy (Morris *et al.*, 2014a) or to the role of ice nucleation activity of microorganisms as an active mechanism for deposition (Morris *et al.*, 2014b). Nevertheless, comparison of the strategies of different small organisms in managing their dispersal could raise questions about common environmental clues such as those signaling the behavior of insects and those signaling the phenological phases of fungi (Delmas *et al.*, 2024), for example.

Chapter 10 presents a perspective on microbial voyages from investigation of environmental archives that have preserved traces of ancient and modern movement of particles in the atmosphere. The most informative of these archives is glacial ice that has captured traces of particles that are deposited mostly with snow but also with dry fall out from major environmental phenomena such as dust storms, volcanic explosions and various anthropic activities including agriculture and burning of fossil fuels. The glacial records that are available for study provide contrasting situations of geographic location with Greenland ice being exposed more intensively to land sources of biological particles compared to Antarctica, for example. The diversity of time scales and particle sources represented in glacial ice is leading to a better understanding of the relative contributions of oceans and land covers to the traffic of particles, to the influence of post-deposition processes on the historical records and to what new dynamics are to be expected with climate change.

⏩ Tools to follow these voyages and assess their significance – Section 3

The ensemble of these incredible voyages is likely to arouse several questions in the minds of the readers. Readers are likely to wonder how to apprehend the voyages of other microbial particles that might be of particular interest to them. They might also wonder about the general fate or impact of these voyages when microbial particles return to the planetary boundary layer. Another critical question might concern actions or strategies to survey these voyages. Pursuit of such questions is the basis for the progress of aerobiology and hence we have devoted chapters in the last section of the book (Chapters 11 to 14) to stimulate these inquiries.

Chapter 11 presents the core set of tools for conceiving and validating dispersal patterns or dissemination trajectories. This chapter begins by addressing how to delimit the windscape in which particles can travel. This can be facilitated by the recently developed Tropolink tool that also permits users to characterize the connectivity of potential sources and sinks within that windscape via the network analyses calculations embedded in the tool. Within this windscape, greater precision about the specific pathways traveled can be obtained via characterization of samples of the organisms of interest. The authors compare demographic approaches to population genetics approaches to this characterization. Demographic methods involve ground-based capture or release-and-re-capture (more amenable to insects than microorganisms) or aerial capture (amenable to microorganisms and insects). Demographic analyses depend, in part, on knowledge of the timing of life cycle phases. Therefore, such analyses might be particularly difficult for bacteria and might eventually be possible for fungi as knowledge of their phenology is perfected (Delmas *et al.*, 2024). Approaches based on population genetics are founded on the diversity of neutral markers, i.e. of genetic loci whose evolution is random. The goal of the different analyses is to assess

the similarity of different populations according to various hypotheses of source, sink, trajectory and the impact of evolution during the dissemination process –all in a background of the overall genetic diversity of the neutral markers. Although these tools are absolutely essential for data analyses, they are equally important as guides to experimental design.

Chapter 12 addresses the fate of aerially-disseminated microbial particles when they fall back to Earth's surface on soil, snow, and water surfaces in particular. The chapter presents a reminder of the initial phase of the voyage into the atmosphere and how this can lead to stratification of particles between the different layers of the troposphere and into the stratosphere. This stratification has consequences on the extent of the voyage and eventual deposition. Those particles in the stratosphere are the most extreme example because they are doomed; there are essentially no natural processes that can lead to their deposition. From the various layers of the troposphere, microbial particles can be deposited via wet or dry processes. This sets off the subsequent fate of the viable immigrants depending on fundamental, down-to-Earth, ecological processes that define invasive capacity. Overall, arrival in pristine environments such as the surfaces of snow or high-altitude lakes, especially when accompanied by massive amounts of dust and biomass, is favorable for success in the new habitats when the immigrating organisms can use local resources and resist local stress. However, even if immigrating microbial voyagers from the atmosphere cannot establish populations in ecosystems where they deposit, the DNA released by their dying cells can become part of the pool available for uptake and transformation.

Chapter 13 reminds us of the relevance of aerobiology to human and animal health by focusing on the microbial nature of the air we breathe. This chapter comes full circle to the first section of the book about the aerodynamics of microbial particles presented in Chapters 2 and 4. Here we see that the physics that reigns particle flight in the free troposphere also reigns particle flight and eventual deposition in lungs. This chapter is also a reminder of the importance of questions about the particulate quality of the air we breathe for the development of air samplers and sampling protocols adapted to microbial particles. This chapter takes us from the typical air-borne flora that can impact human health –the sources and optimal conditions for emissions– to the journey in the lungs and eventually into the blood system. The multiple examples of disease presented in this chapter are stories of invasion where the key factors of success described in Chapter 12 –arrival in a pristine habitat with few competitors, adequate resources and the capacity to overcome local stress– also reign in the human body. The struggle to elucidate the epidemiology of air-borne diseases of humans and animals and to control them has been critically important to the development of aerobiology and to improving human and animal health. However, new ideas are now emerging on the beneficial effects of the microbial passengers of the air we breathe including possible effects on gut health (Fayet-Moore and Robinson, 2024; Liddicoat *et al.*, 2020).

In light of the dynamic nature of the sources of microbial voyagers, of conditions that favor their departure, and of the atmospheric highways themselves, is there an overall framework to guide how we prospect and anticipate the atmospheric comings and goings? This is the question addressed in Chapter 14. This chapter purports that, although the atmosphere is not a habitat *sensu stricto*, it is nevertheless a system to

which concepts about species distribution and diversity can be applied. The authors argue that methods to anticipate atmospheric pathways can be reasoned in the context of the nascent concept of atmospheric biogeography. The attributes of biogeographical distribution can be coupled to meteorological data to construct probable connectivity networks via standard statistical tools for network analysis. As indicated in Chapter 11, this is the basis for the subsequent experimental design and either demographic or population genetics approach to validating these hypotheses. The outcome will be an illustration of the power of another emerging concept –the windshed– where the upwind and downwind catchments represent areas of likely inbound and outbound dispersal. Overlaying the windsheds with geographical maps will certainly reveal a lack of correspondence between geopolitical frontiers and the flight paths of micro-organisms, insects and other small biological particles. Some authors have cheekily labeled the border crossings of air-borne microorganisms as events of legal immigration by alien microorganisms (Weil *et al.*, 2017). Chapter 14 goes beyond the simple statement of fact that transborder dissemination exists to highlight the approaches for states or countries to optimize the effort at surveying and anticipating these dissemination events, with a focus on the surveillance of plant disease spread.

⏩ Literature cited

Amato P., *et al.*, 2017. Active microorganisms thrive among extremely diverse communities in cloud water. *Plos one*, 12, e0182869. https://doi.org/10.1371/journal.pone.0182869

Aylor D.E., 2003. Spread of plant disease on a continental scale: Role of aerial dispersal of pathogens. *Ecology*, 84, 1989-1997. https://doi.org/10.1890/01-0619

Aylor D.E., 2017. Aerial Sampling. *In*: Aylor D.E., ed, *Aerial Dispersal of Pollen and Spores*, APR Press, St. Paul, MN, 339-360. https://doi.org/10.1094/9780890545430.020

Aylor D.E., *et al.*, 2011. Tracking the potato late blight pathogen in the atmosphere using unmanned aerial vehicles and Lagrangian modeling. *Agric. For. Meteorol.*, 151 (2), 251-260. https://doi.org/10.1016/j.agrformet.2010.10.013

Bamou R., *et al.*, 2024. Pathogens spread by high-altitude windborne mosquitoes. *bioRxiv*, https://doi.org/10.1101/2024.12.26.630351

Burrows S.M., *et al.*, 2009a. Bacteria in the global atmosphere – Part 1: Review and synthesis of literature data for different ecosystems. *Atmos. Chem. Phys.*, 9, 9263-9280. https://doi.org/10.5194/acp-9-9263-2009

Burrows S.M., *et al.*, 2009b. Bacteria in the global atmosphere – Part 2: Modelling of emissions and transport between different ecosystems. *Atmos. Chem. Phys.*, 9, 9281-9297. https://doi.org/10.5194/acp-9-9281-2009

Cunliffe M., *et al.*, 2013. Sea surface microlayers: A unified physicochemical and biological perspective of the air–ocean interface. *Progress in Oceanography*, 109, 104-116. https://www.sciencedirect.com/science/article/pii/S0079661112000924

Darwin C.R., 1846. An account of the fine dust which often falls on vessels in the Atlantic Ocean. *Quart. J. Geol. Soc. London*, 2, 26-30. https://darwin-online.org.uk/content/frameset?itemID=F1672&viewtype=text&pageseq=1

Delmas C.E.L., *et al.*, 2024. Monitoring the phenology of plant pathogenic fungi: Why and how? *Biological reviews*, 99 (3), 1075-1084. https://doi.org/10.1111/brv.13058

Després V.R., *et al.*, 2012. Primary biological aerosol particles in the atmosphere: A review. *Tellus B*, 64, 15598. https://doi.org/10.3402/tellusb.v64i0.15598

Domènech M., *et al.*, 2022. What DNA barcodes reveal: Microhabitat preference, hunting strategy and dispersal ability drive genetic variation across Iberian spider species. *Insect Conservation and Diversity*, 15 (2), 248-262. https://doi.org/10.1111/icad.12552

Fayet-Moore F., Robinson S.R., 2024. A breath of fresh air: Perspectives on inhaled nutrients and bacteria to improve human health. *Advances in Nutrition*, 15 (12), 100333. https://www.sciencedirect.com/science/article/pii/S2161831324001674

Fröhlich-Nowoisky J., *et al*., 2016. Bioaerosols in the Earth system: Climate, health, and ecosystem interactions. *Atmospheric Research*, 182, 346-376. https://www.sciencedirect.com/science/article/pii/S0169809516301995

Gregory P.H., 1961. *The Microbiology of the Atmosphere*, Interscience Publishers, New York. https://doi.org/10.5962/bhl.title.7291

Henderson T.J., Salem H., 2016. The Atmosphere: Its developmental history and contributions to microbial evolution and habitat. *In*: Henderson T.J., Salem H., eds, *Aerobiology: The Toxicology of Airborne Pathogens and Toxins*, *Royal Society of Chemistry*, 1-41. https://doi.org/10.1039/9781849737913-00001

Kobziar L.N., *et al*., 2018. Pyroaerobiology: The aerosolization and transport of viable microbial life by wildland fire. *Ecosphere*, 9 (11), e02507. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.2507

Kobziar L.N., *et al*., 2024. Principles of fire ecology. *Fire Ecology*, 20 (1), 39. https://doi.org/10.1186/s42408-024-00272-0

Lappan R., *et al*., 2024. The atmosphere: A transport medium or an active microbial ecosystem? *ISME J.*, 18 (1), wrae092. https://doi.org/10.1093/ismejo/wrae092

Liddicoat C., *et al*., 2020. Naturally-diverse airborne environmental microbial exposures modulate the gut microbiome and may provide anxiolytic benefits in mice. *Sci. Tot. Environ*, 701, 134684. https://www.sciencedirect.com/science/article/pii/S0048969719346753

Lighthart B., Shaffer B.T., 1994. Bacterial flux from chaparral into the atmosphere in mid-summer at a high desert location. *Atmos. Sci*., 28, 1267-1274. https://doi.org/10.1016/1352-2310(94)90273-9

Lindemann J., *et al*., 1982. Plants as source of airbone bacteria, including ice nucleation-active bacteria. *Appl. Environ. Microbiol*., 44, 1059-1063. http://www.ncbi.nlm.nih.gov/pmc/articles/PMC242148/

Mccubbin W.A., 1944. Relation of spore dimension to their rate of fall. *Phytopathology*, 34, 230-234.

Miguel M.P., 1883. *Les organismes vivants de l'atmosphère*, Gauthier-Villars, Paris, 310. Review: https://www.science.org/doi/10.1126/science.ns-3.64.518

Morris C.E., Martinetti D., 2023. Des sentinelles sur les autoroutes aériennes d'agents phytopathogènes. *In*: Lannou C., *et al*., eds, *Crises sanitaires en agriculture. Les espèces invasives sous surveillance*, Versailles, éditions Quæ, 203-218.

Morris C.E., *et al*., 2014a. Movement of bioaerosols in the atmosphere and the consequences for climate and microbial evolution (Chapter 16). *In*: Colbeck I., Lazaridis M., eds, *Aerosol Science: Technology and Applications*, John Wiley & Sons, Ltd., 393-416. https://doi.org/10.1002/9781118682555.ch16

Morris C.E., *et al*., 2014b. Bioprecipitation: A feedback cycle linking Earth history, ecosystem dynamics and land use through biological ice nucleators in the atmosphere. *Global Change Biol*., 20, 341-351. https://doi.org/10.1111/gcb.12447

Radici A., *et al*., 2022. Early-detection surveillance for stem rust of wheat: Insights from a global epidemic network based on airborne connectivity and host phenology. *Environ. Res. Lett.*, 17 (6), 064045. https://dx.doi.org/10.1088/1748-9326/ac73aa

Sesartic A., Dallafior T.N., 2011. Global fungal spore emissions, review and synthesis of literature data. *Biogeosciences*, 8, 1181-1192. https://doi.org/10.5194/bg-8-1181-2011

Stakman E., Christensen C.M., 1946. Aerobiology in relation to plant disease. *Botanical Review*, 12 (4), 205-253. https://www.jstor.org/stable/4353339

Stakman E.C., *et al*., 1923. Spores in the upper air. *J. Agric. Res*., 24, 599-606.

Stopelli E., *et al*., 2017. Ice nucleators, bacterial cells and *Pseudomonas syringae* in precipitation at Jungfraujoch. *Biogeosciences*, 14 (5), 1189-1196. https://doi.org/10.5194/bg-14-1189-2017

Weil T., *et al*., 2017. Legal immigrants: Invasion of alien microbial communities during winter occurring desert dust storms. *Microbiome*, 5 (1), 32. http://dx.doi.org/10.1186/s40168-017-0249-7

Wolf F.T., 1943. The microbiology of the upper air. *Bull. Torrey Botan. Club*, 70, 1-14. https://www.jstor.org/stable/2481676

Section 1

The nature of atmospheric highways and principles for understanding how microbial particles can ride them

Chapter 1

Air mass movement across Earth: Highways for particle transport in the past, present and future

Fabrice Lambert

Modern air mass circulation patterns

Understanding modern air mass circulation patterns is fundamental to comprehending how Earth's atmosphere functions and influences microparticle transport pathways. These patterns, driven by the uneven heating of the Earth's surface and the rotation of the planet, create distinct wind systems that transport heat, moisture, and particles across the globe. This chapter delves into the primary circulation and wind patterns that shape the dispersal of particles. Knowledge of dispersal is founded primarily on studies of mineral dust aerosols. However, it is well known that spores, microbes, and viruses can attach to mineral dust particles through various mechanisms, including electrostatic forces and physical entrapment within the dust matrix (Smith *et al.*, 2011). Furthermore, carbonaceous materials, organic compounds, smoke, and even sea salt can carry microorganisms. The range of processes of emission of particles that harbor living microorganisms, including dust and sea-spray emissions, emissions from other surface waters and via fires, are covered primarily in Chapters 3, 4, 7 and 8. The association of microorganisms with dust or other particles may contribute to their survival (Noda *et al.*, 2023), which can be assessed from various approaches as described in Chapter 6. Nevertheless, the emissions processes all contribute to assuring that microorganisms can ride the dust transport systems. By exploring these dust transport systems, we gain insight into the mechanisms that govern atmospheric dynamics and their critical role in the dispersal of spores, microbes, and viruses.

The Easterlies

The Easterlies, also known as the trade winds, are a prominent component of Earth's atmospheric circulation. These winds influence the El Niño Southern Oscillation, the South Asian, African, and American monsoon systems, and notably the transport of Saharan dust across the Atlantic Ocean.

Structure and mechanism

The Easterlies are surface winds that blow from the east towards the west. They are found in the tropical regions, between approximately 30 degrees latitude and the equator in both hemispheres (Figure 1.1). The formation of the Easterlies is closely linked to the Hadley Cell circulation.

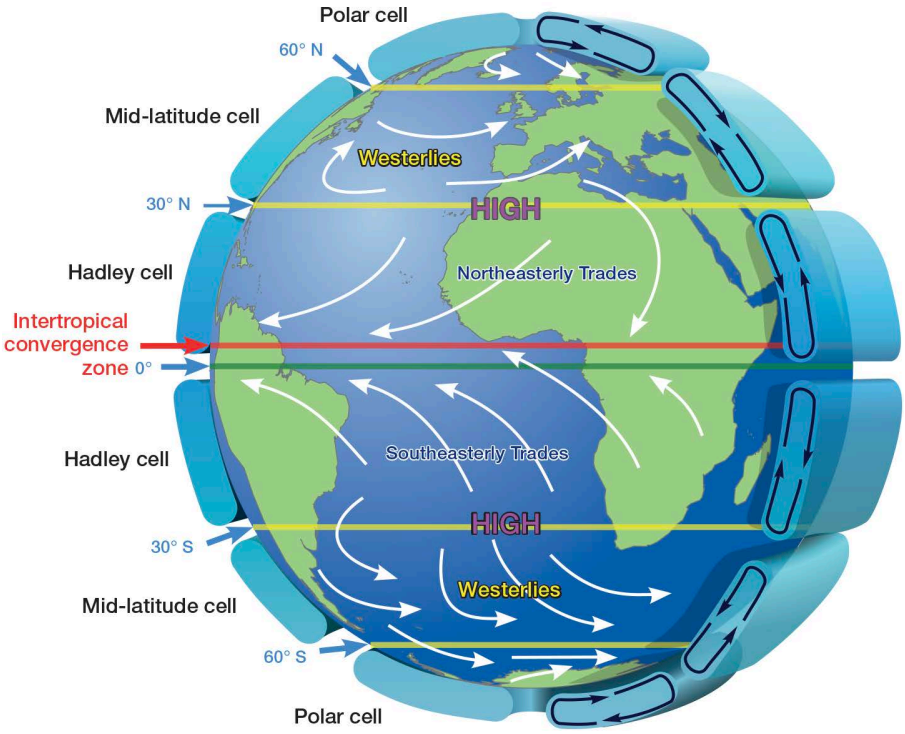


Figure 1.1. Earth Global Circulation. Source: Wikimedia Commons, Kaidor / CC-BY-SA-3.0.

The Hadley Cell is a large-scale atmospheric circulation pattern that operates between the equator and approximately 30 degrees latitude in both hemispheres (Figure 1.1). The process begins with the intense solar heating at the equator, causing warm, moist air to rise. As this air ascends, it cools and condenses, forming towering cumulonimbus clouds and resulting in heavy rainfall, which is typical of equatorial regions and identifies the location of the Intercontinental Convergence Zone.

Once the air reaches the upper troposphere, it diverges towards the poles. Around 30 degrees latitude, the now cooler and drier air descends, creating high-pressure zones known as the subtropical highs. This descending air warms adiabatically, leading to the arid conditions and the formation at these latitudes of most of the world's deserts, such as the Sahara in North Africa and the Gobi and Taklimakan Deserts in East Asia.

The surface winds that return towards the equator from these high-pressure zones are deflected westward by the Coriolis effect, forming the Easterlies. These winds are most consistent and strongest over the oceans, where there are fewer obstacles to disrupt their flow.

Implications for long-range transport

The Easterlies are located close to the subtropical desertic areas that are the main sources of dust to the atmosphere (Kok *et al.*, 2021). These winds facilitate the movement of dust particles over vast distances, impacting regions far from their source:
– Each summer, the Saharan Air Layer carries massive amounts of mineral dust from the Sahara Desert westward over the Atlantic Ocean. The Easterlies drive this transport, allowing dust particles to travel thousands of kilometers. This dust can reach as far as the Caribbean, the Americas, and even parts of the southeastern United States (Bi *et al.*, 2024). The transport of Saharan dust is a key component of the global dust cycle and has significant implications for various regions and ecosystems (Bristow *et al.*, 2010; Francis *et al.*, 2020). Dust emissions in North Africa occur all year round with a peak during boreal summer (Maher *et al.*, 2010).
– In some cases, the Easterlies can contribute to dust transport in regions like India. For example, during certain dust storms, strong easterly winds can lift dust from the Thar Desert and transport it across northern India (Banerjee *et al.*, 2021). Dust activity in India peaks during boreal spring (Maher *et al.*, 2010).

The Westerlies

The Westerlies, or Northern and Southern Westerly winds (NWW and SWW, respectively), are another major component of Earth's atmospheric circulation. These winds play a critical role in shaping the climate and weather patterns of mid-latitude regions and have significant implications for the dispersal of dust and biological particles.

Structure and mechanism

The Westerlies are surface winds that blow from the west towards the east. They are found in the mid-latitudes, between approximately 30 and 60 degrees latitude in both hemispheres (Figure 1.1). The formation of the Westerlies is closely linked to the Ferrel Cell and the Polar Cell circulation patterns.

The Ferrel Cell operates between approximately 30 and 60 degrees latitude in both hemispheres (Figure 1.1). Unlike the Hadley and Polar Cells, which are driven primarily by thermal forces, the Ferrel Cell is largely influenced by the interactions between the other two cells and the Coriolis effect. In the Ferrel Cell, surface air moves poleward from the subtropical high-pressure zones at around 30 degrees latitude. As this air travels towards higher latitudes, it is deflected eastward by the Coriolis effect, forming the Westerlies. These winds are strongest and most consistent over the oceans, and sometimes merge with the polar jet streams to form westerly flow across the whole height of the troposphere.

The Polar Cell operates between approximately 60 degrees latitude and the poles in both hemispheres (Figure 1.1). This cell is driven primarily by the cold, dense air at the poles, which creates high-pressure zones. At the poles, the cold air sinks and spreads out towards lower latitudes. As this air moves away from the poles, it is deflected westward by the Coriolis effect, forming the polar easterlies. These surface winds flow towards the equator until they meet the warmer air from the Ferrel Cell at around 60 degrees latitude, creating the Polar Front. Here, the warmer air from the Ferrel Cell rises over the colder polar air, leading to the formation of mid-latitude cyclones and other weather phenomena.

Cyclones are large air masses that rotate around a strong center of low atmospheric pressure. In the mid-latitudes, extratropical cyclones are a common feature and are driven by the interactions between the Westerlies and the polar Easterlies. These cyclones typically form along the Polar Front, where the contrasting air masses meet and rotate around the poles following the westerly winds. Cyclones can entrain dust and other particles from the surface through several mechanisms (Liu *et al.*, 2003): Strong surface winds associated with cyclones can lift dust particles from the surface into the lower troposphere. Dust particles can only escape the lowest surface layer when a minimum wind speed threshold is surpassed (Kurosaki and Mikami, 2007). Within the cyclone, strong updrafts can carry these dust particles from the lower troposphere several kilometers high into the upper levels. These updrafts are particularly strong in the warm conveyor belt, a region of rising air on the eastern side of the cyclone. As the cyclone moves, it can lift air masses along its frontal boundaries, further aiding in the vertical transport of dust particles.

Once in the higher troposphere, these dust particles can be picked up by the prevailing winds and transported over several thousand kilometers, significantly impacting regions far from their source (Struve *et al.*, 2020).

Implications for long-range transport

The Northern and Southern Westerly winds play a key role in the long-range transport of dust sourced from the northern and southern mid-latitudes. Two notable examples are the transport of East Asian dust towards the North Pacific and North America all the way to Greenland (Serno *et al.*, 2015), and the transport of dust from Australia, New Zealand, and Patagonia over the Southern Oceans and Antarctica (Albani *et al.*, 2012; Kok *et al.*, 2021):

– East Asia is one of the world's largest sources of dust, particularly from the Taklimakan and Gobi Deserts. During dust storms, these particles are lifted into the atmosphere and can be transported across the Pacific Ocean by the Westerlies. This transpacific transport can carry dust particles thousands of kilometers, reaching as far as North America (Guo *et al.*, 2017). Dust storms over East Asian deserts occur mainly during boreal spring (Yang *et al.*, 2021).

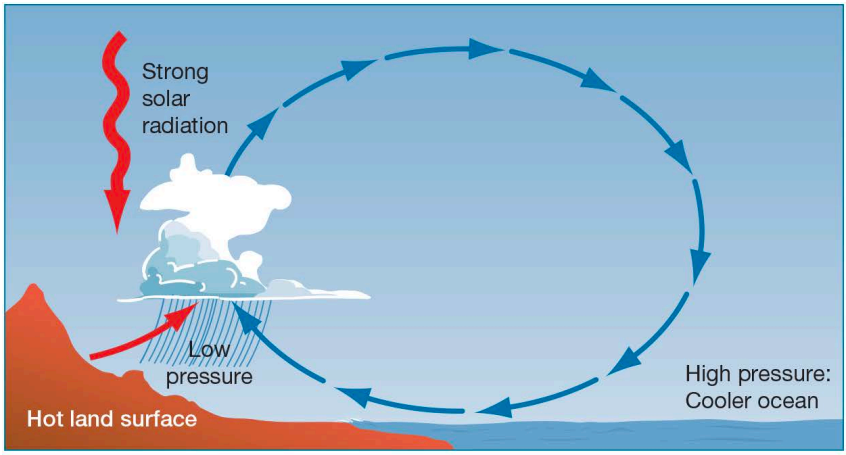
– In the Southern Hemisphere, dust from Australia, New Zealand, and Patagonia is transported over the Southern Oceans by the Westerlies (Neff and Bertler, 2015). This dust plays a pivotal role in the biogeochemical cycles of the Southern Ocean. For example, Patagonian dust is a significant source of iron, which is a limiting nutrient for phytoplankton growth in the high-nutrient, low-chlorophyll waters of the Southern Ocean (Johnson *et al.*, 2011). Southern mid-latitude dust is emitted throughout the year, with a maximum during austral summer in southern South America (Cosentino *et al.*, 2021) and a maximum during austral winter in Australia (Marx *et al.*, 2005).

The monsoons

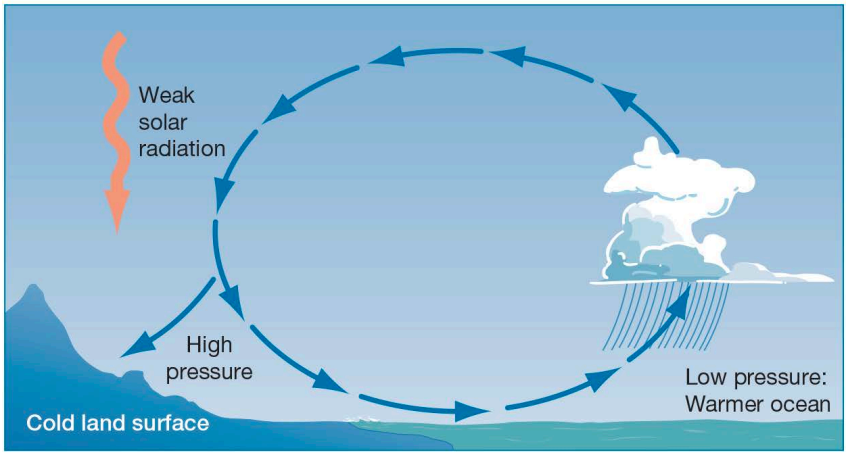
Monsoons are seasonal wind patterns that bring significant changes in weather, particularly in tropical and subtropical regions. These winds are characterized by a dramatic shift in direction between the wet and dry seasons, profoundly impacting the climate and ecosystems of affected areas (IPCC, 2021a).

Structure and mechanism

Monsoons are driven by the differential heating of land and sea. During the summer, the land heats up more quickly than the ocean, creating a low-pressure area over the land and a high-pressure area over the ocean (Figure 1.2A). This pressure difference causes moist air from the ocean to flow towards the land, bringing heavy rainfall.



A) Summer monsoon



B) Winter monsoon

Figure 1.2. Atmospheric circulation during the summer and winter monsoon (Ruddiman, 2008).

In the winter, the situation reverses. The land cools down more quickly than the ocean, creating a high-pressure area over the land and a low-pressure area over the ocean (Figure 1.2B). This causes dry air to flow from the land towards the ocean, leading to dry conditions over the land. The winter monsoon is particularly strong in regions such as East Asia, where it is known as the East Asian Winter Monsoon (EAWM).

Implications for long-range transport

During the winter monsoon, dry, strong winds can entrain dust from arid and semi-arid regions and transport it over vast distances. Two notable examples are the transport of dust from East Asia and the Indian subcontinent:
– The EAWM is a significant driver of dust transport in East Asia. During the winter, strong northerly winds blow from the high-pressure system over Siberia towards the low-pressure areas over the Pacific Ocean. These winds can lift dust particles from the deserts of northern China and Mongolia, such as the Gobi and Taklimakan Deserts. The dust is then transported southward and eastward, reaching as far as the Korean Peninsula, Japan, and even the North Pacific Ocean (Yang *et al.*, 2021). The dust particles can then be picked up by the Northern Westerly winds and transported further towards North America.
– During the winter monsoon, dry northeasterly winds blow from the Indian subcontinent towards the Indian Ocean. These winds can entrain dust from arid regions in India and neighbouring countries. The dust is transported over the Indian Ocean, where it can join the Easterly winds and be transported towards Africa (Li and Ramanathan, 2002).

⏩ Impact of climate change on circulation patterns

Climate change is profoundly altering the dynamics of Earth's atmosphere, leading to significant shifts in air mass circulation patterns (IPCC, 2021b). These changes have far-reaching implications for global climate, weather systems, and the dispersal of mineral and biological particles. This chapter examines how climate change is impacting key atmospheric circulation patterns, including the Easterlies, Westerlies, and Monsoons. By exploring both past (paleoclimatic) empirical data and future simulated projections from the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (AR6) scenarios, we gain a comprehensive understanding of the evolving nature of these wind systems and their potential consequences for ecosystems and human societies.

Changes in the Easterlies

The strength and position of the Easterlies is closely linked with the position of the main climatic cells, the Intertropical Convergence Zone, and the latitudinal temperature gradient of the Earth. These are not fixed features of the climatic system, but are influenced by the location and shape of the continents, and climate change. These winds have changed in the past and they are expected to be influenced by modern climate change and global warming.

Paleoclimatic changes

Paleoclimatic records provide valuable insights into the historical variability of the Easterlies. During the Last Glacial Maximum (LGM), approximately 21,000 years ago, the trade winds were generally stronger and more extensive than they are today. This was due to the larger temperature gradients between the equator and the poles, which intensified the atmospheric circulation patterns (Kim *et al.*, 2003; Stuut *et al.*, 2002).

Evidence from marine sediments, ice cores, and other paleoclimate proxies indicates that the strength and position of the Easterlies have fluctuated significantly

over millennia (Kim *et al.*, 2003). For example, during the Holocene epoch (the last 11,700 years), there have been periods of both stronger and weaker trade winds, influenced by factors such as volcanic activity, solar radiation variations, and changes in Earth's orbit (Stuut *et al.*, 2002).

Future changes

The IPCC AR6 projects that future changes in the Easterlies will be influenced by ongoing global warming and associated shifts in atmospheric circulation patterns. Under various greenhouse gas emission scenarios, the trade winds are expected to undergo significant changes by the end of the 21st century (IPCC, 2021b):

– The strength of the Easterlies is projected to weaken in some regions, particularly in the Pacific Ocean, due to the reduced temperature gradient between the equator and the poles. This weakening could lead to changes in ocean circulation patterns, such as a reduction in upwelling, which would impact marine ecosystems and fisheries (IPCC, 2023a).
– The seasonal variability of the Easterlies is also expected to increase. This means that the intensity and position of the trade winds could vary more dramatically between seasons, potentially leading to more extreme weather events, such as stronger tropical cyclones and altered precipitation patterns (IPCC, 2023a).
– The impact of climate change on the Easterlies will not be uniform across the globe. Some regions may experience more pronounced changes than others, depending on local climatic conditions and feedback mechanisms. For example, the Atlantic trade winds might weaken less than those in the Pacific, leading to different regional climate impacts (IPCC, 2023a).

Implications for long-range transport

Climate change may significantly impact the long-range transport of Saharan dust by altering the strength and patterns of the Easterlies. Climate change may weaken the Easterlies in some regions, potentially reducing the transport of Saharan dust (IPCC, 2021b). However, increased desertification and reduced vegetation cover in the Sahel region could enhance dust emissions, leading to complex changes in dust transport dynamics (Mahowald, 2007).

Dust concentrations are projected to decrease in India during the 21st century, but the role of the Easterlies in this change is unclear (Pu and Ginoux, 2018).

Changes in the Westerlies

The strength and position of the Northern and Southern Westerly winds is strongly influenced by the latitudinal temperature gradient of the Earth and the position of the Polar Front. There is substantial evidence that these variables have fluctuated during past climate change, in particular for the SWW (Kohfeld *et al.*, 2013). In the future, global warming and polar amplification may influence the position and strength of these winds, although the uncertainties are high (IPCC, 2023a).

Paleoclimatic changes

During the LGM, approximately 21,000 years ago, the Westerlies were generally stronger and shifted equatorward (IPCC, 2023b; Kohfeld *et al.*, 2013; Wang *et al.*, 2018).

This shift was associated with the expansion of ice sheets, sea-ice, and changes in sea surface temperatures. Throughout the Holocene epoch (the last 11,700 years), the position and intensity of the Westerlies have fluctuated to a lesser degree (Lamy *et al.*, 2010; Li and Zhang, 2020), and with evidence that is sometimes conflicting concerning the direction of change (Fletcher and Moreno, 2012; Villacís *et al.*, 2023). These changes were influenced by variations in solar radiation, volcanic activity, and oceanic conditions.

Future changes

Future changes in the Westerlies will be influenced by ongoing global warming and associated shifts in atmospheric circulation patterns (IPCC, 2021b):
– The strength of the Westerlies is projected to increase in the upper troposphere, particularly in the Southern Hemisphere, due to the enhanced temperature gradient between the equator and the poles. However, near the surface, the Westerlies may weaken in some regions due to changes in the distribution of land and sea temperatures (IPCC, 2023a). Both the SWW and the NWW may shift polewards due to climate change, although with less certainty in the northern Hemisphere (IPCC, 2023a, 2023c).
– The seasonal variability of the Westerlies is expected to increase, with more pronounced shifts between summer and winter positions. This could lead to more extreme weather events, such as stronger storms and altered precipitation patterns (IPCC, 2023a).
– The impact of climate change on the Westerlies will not be uniform across the globe. For example, the Southern Hemisphere Westerlies are projected to shift poleward, leading to changes in precipitation patterns in regions such as southern Australia and South America. In the Northern Hemisphere, the response of the Westerlies is stronger in the Pacific sector than in the Atlantic (IPCC, 2023a).

Implications for long-range transport

The Westerlies facilitate the transport of dust from East Asia, especially from the Taklimakan and Gobi Deserts, across the North Pacific Ocean. Climate change is projected to alter the strength and position of the Westerlies, potentially increasing the frequency and intensity of dust storms and shifting associated weather patterns in the west coast of North America.

In the Southern Hemisphere, the Westerlies are responsible for transporting dust from regions such as Australia, New Zealand, and Patagonia over the Southern Oceans. Climate-induced changes in the Westerlies, including a poleward shift and increased variability, could modify dust and microorganism transport patterns.

Changes in the Westerlies will have significant implications for the dispersal of spores, microbes, and viruses. Stronger and more variable Westerlies could enhance the long-distance transport of these biological particles, potentially altering the distribution of species and affecting ecosystems far from their point of origin. Conversely, shifts in the position of the Westerlies could lead to changes in the regions affected by these winds, impacting local climates and biological processes.

Changes in the monsoons

Monsoons are critical for the climate and weather patterns of many tropical and subtropical regions. Understanding how these seasonal wind patterns have changed

in the past and how they might change in the future is essential for predicting their impact on climate and biological dispersal.

Paleoclimatic changes

Monsoon systems have experienced significant fluctuations in intensity and extent over glacial-interglacial cycles, with a weaker (stronger) monsoon during cold (warm) times being observed in paleoclimatic records. These changes were driven mostly by changes in Earth's orbit, known as Milankovitch cycles (IPCC, 2023b).

During the mid-Holocene (around 6,000 years ago), the African and Asian monsoons were generally stronger and more extensive than they are today. This period, known as the Holocene Climatic Optimum, was characterized by increased solar radiation in the Northern Hemisphere summer, which enhanced the land-sea temperature contrast and strengthened monsoon circulation. Conversely, during periods of reduced solar radiation, such as the Little Ice Age (approximately 1300 to 1850 AD), monsoon systems weakened. This weakening was associated with cooler global temperatures and reduced land-sea temperature contrasts (Seth *et al.*, 2019).

Future changes

The IPCC AR6 scenarios project that future changes in monsoons will be influenced by ongoing global warming and associated shifts in atmospheric circulation patterns (IPCC, 2021b):
– The intensity and extent of monsoon systems are projected to increase in many regions due to the enhanced land-sea temperature contrast caused by global warming. This is expected to lead to more intense and widespread monsoon rains, particularly in South Asia, East Asia, and West Africa (IPCC, 2023a).
– The seasonal variability of monsoons is also expected to increase. This means that the timing and intensity of monsoon rains could become more erratic, leading to more frequent and severe droughts and floods (IPCC, 2023a).
– The impact of climate change on monsoons will not be uniform across the globe. For example, while the South Asian monsoon is projected to become stronger and wetter, the North American monsoon might experience a reduction in rainfall due to changes in atmospheric circulation and moisture availability (IPCC, 2023a).

Implications for long-range transport

Climate change significantly impacts the entrainment and transport of dust through the winter monsoon winds. Through the winter monsoon, characterized by strong and dry winds, dust is lifted and transported from arid and semi-arid regions over vast distances:
– The EAWM is a major driver of dust transport in East Asia. Climate change is projected to alter the intensity and patterns of the EAWM, potentially increasing the frequency and strength of dust storms. Enhanced dust entrainment from the Gobi and Taklimakan Deserts can lead to higher dust concentrations being transported southward and eastward, affecting regions such as the Korean Peninsula, Japan, the North Pacific Ocean and North America.
– During the winter monsoon, dry northeasterly winds blow from the Indian subcontinent towards the Indian Ocean. Climate change may intensify these winds, increasing the entrainment of dust from arid regions in India and neighbouring countries.

Conclusions

This chapter has explored the primary atmospheric circulation patterns, including the Easterlies, Westerlies, and Monsoons, which are fundamental in shaping the global distribution of dust and biological particles. The successful transport of biological particles via these atmospheric highways depends on the characteristics that define their aerodynamic properties (Chapter 2) and capacity to remain viable (Chapter 6). Transport can assure geographical expansion of microbial populations arising from the immigrating biological particles depending on resilience and adaptability as illustrated in Chapter 12.

The Easterly winds facilitate the long-range transport of Saharan dust across the Atlantic, influencing ecosystems far from their source. The Westerly winds allow the transpacific transport of East Asian dust and the movement of dust from the Southern Hemisphere continents to the Southern Ocean and Antarctica. The interaction between cyclones and dust transport underscores the dynamic nature of these wind systems. Monsoon winds significantly impact dust transport, particularly during the winter in East Asia and the Indian subcontinent.

In the future, climate change is expected to alter the strength and position of the Easterly winds, potentially reducing dust transport in some regions while increasing it in others due to enhanced desertification. The Westerly winds are projected to strengthen and shift poleward. These changes will affect dust transport dynamics, particularly across the North Pacific and Southern Oceans. Future monsoon systems are also expected to intensify and show more variable patterns. This will lead to more extreme weather events, impacting dust entrainment and transport.

Literature cited

Albani S., *et al.*, 2012. Comparing modeled and observed changes in mineral dust transport and deposition to Antarctica between the Last Glacial Maximum and current climates. *Clim. Dyn.,* 38, 1731-1755. https://doi.org/10.1007/s00382-011-1139-5

Banerjee P., *et al.*, 2021. The unusual severe dust storm of May 2018 over northern India: Genesis, propagation, and associated conditions. *J. Geophys. Res.: Atmospheres,* 126, e2020JD032369. https://doi.org/10.1029/2020JD032369

Bi H., *et al.*, 2024. The circumglobal transport of massive African dust and its impacts on the regional circulation in remote atmosphere. *Bull. Am. Meteorol. Soc.,* 105, E605-E622. https://doi.org/10.1175/BAMS-D-23-0072.1

Bristow C.S., *et al.*, 2010. Fertilizing the Amazon and equatorial Atlantic with West African dust. *Geophys. Res. Lett.,* 37. https://doi.org/10.1029/2010GL043486

Cosentino N.J., *et al.*, 2021. Present-day Patagonian dust emissions: Combining surface visibility, mass flux, and reanalysis data. *J. Geophys. Res.: Atmospheres,* 126, 1-18. https://doi.org/10.1029/2020JD034459

Fletcher M.S., Moreno P.I., 2012. Have the Southern Westerlies changed in a zonally symmetric manner over the last 14,000 years? A hemisphere-wide take on a controversial problem. *Quaternary International,* 253, 32-46. https://doi.org/10.1016/J.QUAINT.2011.04.042

Francis D., *et al.*, 2020. The atmospheric drivers of the major Saharan dust storm in June 2020. *Geophys. Res. Lett.,* 47, e2020GL090102. https://doi.org/10.1029/2020GL090102

Guo J., *et al.*, 2017. Trans-Pacific transport of dust aerosols from East Asia: Insights gained from multiple observations and modeling. *Environmental Pollution,* 230, 1030-1039. https://doi.org/10.1016/J.ENVPOL.2017.07.062

IPCC, 2023a. Future global climate: Scenario-based projections and near-term information. *Climate Change 2021 – The Physical Science Basis*, 553-672. https://doi.org/10.1017/9781009157896.006

IPCC, 2023b. Changing state of the climate system. *Climate change 2021 – The Physical Science Basis*, 287-422. https://doi.org/10.1017/9781009157896.004

IPCC, 2023c. Water cycle changes. *Climate change 2021 – The Physical Science Basis*, 1055-1210. https://doi.org/10.1017/9781009157896.010

IPCC, 2021a. Annex V: Monsoons. *Climate Change 2021: The Physical Science Basis*. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2193-2204. https://doi.org/10.1017/9781009157896.019

IPCC, 2021b. IPCC AR6 Working Group 1: Summary for Policymakers. *Climate Change 2021: The Physical Science Basis.* Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 3-32. https://doi.org/10.1017/9781009157896.001

Johnson M.S., *et al*., 2011. Understanding the transport of Patagonian dust and its influence on marine biological activity in the South Atlantic Ocean. *Atmos. Chem. Phys.,* 11, 2487-2502. https://doi.org/10.5194/ACP-11-2487-2011

Kim J.-H., *et al.*, 2003. Reconstruction of SE trade-wind intensity based on sea-surface temperature gradients in the Southeast Atlantic over the last 25 kyr. *Geophys. Res. Lett.,* 30, 2144. https://doi.org/10.1029/2003GL017557

Kohfeld K.E., *et al*., 2013. Southern Hemisphere westerly wind changes during the Last Glacial Maximum: Paleo-data synthesis. *Quat. Sci. Rev.,* 68, 76-95. https://doi.org/10.1016/j.quascirev.2013.01.017

Kok J.F., *et al*., 2021. Contribution of the world's main dust source regions to the global cycle of desert dust. *Atmos. Chem. Phys.,* 21, 8169-8193. https://doi.org/10.5194/ACP-21-8169-2021

Kurosaki Y., Mikami M., 2007. Threshold wind speed for dust emission in east Asia and its seasonal variations. *J. Geophys. Res.: Atmospheres,* 112, 17202. https://doi.org/10.1029/2006JD007988

Lamy F., *et al*., 2010. Holocene changes in the position and intensity of the southern westerly wind belt. *Nat. Geosci.,* 3, 695-699. https://doi.org/10.1038/ngeo959

Li F., Ramanathan V., 2002. Winter to summer monsoon variation of aerosol optical depth over the tropical Indian Ocean. *J. Geophys. Res.: Atmospheres,* 107, AAC 2-1. https://doi.org/10.1029/2001JD000949

Li Y., Zhang Y., 2020. Synergy of the westerly winds and monsoons in the lake evolution of global closed basins since the Last Glacial Maximum and implications for hydrological change in central Asia. *Climate of the Past,* 16, 2239-2254. https://doi.org/10.5194/CP-16-2239-2020

Liu M., *et al.*, 2003. A high-resolution numerical study of the Asian dust storms of April 2001. *J. Geophys. Res.: Atmospheres,* 108, 8653. https://doi.org/10.1029/2002JD003178

Maher B.A., *et al*., 2010. Global connections between aeolian dust, climate and ocean biogeochemistry at the present day and at the last glacial maximum. *Earth Sci. Rev.,* 99, 61-97. https://doi.org/10.1016/j.earscirev.2009.12.001

Mahowald N.M., 2007. Anthropocene changes in desert area: Sensitivity to climate model predictions. *Geophys. Res. Lett.,* 34, L18817. https://doi.org/10.1029/2007GL030472

Marx S.K., *et al*., 2005. Estimates of Australian dust flux into New Zealand: Quantifying the eastern Australian dust plume pathway using trace element calibrated 210Pb as a monitor. *Earth Planet Sci. Lett.,* 239, 336-351. https://doi.org/10.1016/J.EPSL.2005.09.002

Neff P.D., Bertler N.A.N., 2015. Trajectory modeling of modern dust transport to the Southern Ocean and Antarctica. *J. Geophys. Res.: Atmospheres* 120, 9303-9322. https://doi.org/10.1002/2015JD023304

Noda J., *et al*., 2023. Dust and microorganisms: Their interactions and health effects. *In*: Al-Dousari A., Hashmi M.Z. (eds) *Dust and Health. Emerging Contaminants and Associated Treatment Technologies*. Springer, 137-156. https://doi.org/10.1007/978-3-031-21209-3_8

Pu B., Ginoux P., 2018. How reliable are CMIP5 models in simulating dust optical depth? *Atmos. Chem. Phys.,* 18, 12491-12510. https://doi.org/10.5194/ACP-18-12491-2018

Ruddiman W.F., 2008. *Earth's Climate: Past and Future*. Second Edition, W.H. Freeman and Company, New York.

Serno S., *et al*., 2015. Comparing dust flux records from the Subarctic North Pacific and Greenland: Implications for atmospheric transport to Greenland and for the application of dust as a chronostratigraphic tool. *Paleoceanography,* 30, 583-600. https://doi.org/10.1002/2014PA002748

Seth A., *et al*., 2019. Monsoon responses to climate changes. Connecting past, present and future. *Current Climate Change Reports,* 5 (25), 63-79. https://doi.org/10.1007/S40641-019-00125-Y

Smith D.J., *et al*., 2011. The high life: Transport of microbes in the atmosphere. *Eos, Transactions American Geophysical Union,* 92, 249-250. https://doi.org/10.1029/2011EO300001

Struve T., *et al*., 2020. A circumpolar dust conveyor in the glacial Southern Ocean. *Nat. Comm.*,11, 1-11. https://doi.org/10.1038/s41467-020-18858-y

Stuut J.B.W., *et al*., 2002. A 300-kyr record of aridity and wind strength in southwestern Africa: Inferences from grain-size distributions of sediments on Walvis Ridge, SE Atlantic. *Mar. Geol.,* 180, 221-233. https://doi.org/10.1016/S0025-3227(01)00215-8

Villacís L.A., *et al*., 2023. A freshwater diatom perspective on the evolution of the southern westerlies for the past ~14,000 years in southwestern Patagonia. *Quat. Sci. Rev.,* 301, 107929. https://doi.org/10.1016/J.QUASCIREV.2022.107929

Wang N., *et al*., 2018. Northern Westerlies during the Last Glacial Maximum: Results from CMIP5 Simulations. *J. Clim.,* 31, 1135-1153. https://doi.org/10.1175/JCLI-D-17-0314.1

Yang L., *et al*., 2021. Distinct effects of winter monsoon and westerly circulation on dust aerosol transport over East Asia. *Theor. Appl. Climatol.,* 144, 1031-1042. https://doi.org/10.1007/S00704-021-03579-Z/METRICS

Chapter 2

A primer on the aerodynamic traits of microbial particles that define their capacity for dispersal

Cindy E. Morris

Microbial particles –single cells, cell aggregates, spores, hyphal filaments, etc.– can be emitted into the atmosphere by active projectile mechanisms or abrasion from air currents (Aylor, 2017). After this departure from ground-level habitats, the effective aerial dispersal of microorganisms to distant habitats depends on both their physical and biological traits. In general, physical traits determine the capacity for passive flight along atmospheric highways whereas biological traits foster survival in face of the environmental conditions encountered along the trajectory. This chapter will focus on the physical traits of microbial particles that define their capacity to ride atmospheric highways. As illustrated in Chapters 12 and 14, the trajectories of dissemination of microbial particles via the atmosphere are mostly inferred rather than observed directly. To estimate by inference the expansiveness of long-distance aerial dissemination and the possible trajectories, knowledge of aerodynamic properties of particles is set into the context of weather conditions and any factors that promote particle release and entry into more turbulent air. However, for microorganisms, in spite of the availability of methods to directly measure their key aerodynamic properties, their physical dimensions have often been used as a proxy. This chapter will explain how traits such as size, shape, specific density, ornamentation and state of hydration contribute to the gravitational and drag forces on particles as they move through the air and can confound predictions about aerodynamic properties that are based simply on particle size. The information below is presented in a manner accessible for biologists with intuitive explanations of physical phenomena where possible.

⏩ Terminal velocity: Defying gravity

Still air appears to offer little resistance to the movement of most macroscopic objects. However, air is a fluid with a certain amount of viscosity, i.e. the capacity to resist movement of solid objects. When an object falls in still air, its acceleration due to gravity confronts the drag from the viscosity of air. As pointed out by Gregory (1961) in his classic and groundbreaking treatise on *The Microbiology of the Atmosphere*, "still air" is a vague description but generally refers to air moving at < 1 cm/sec for indoors

conditions and < 10 cm/sec for outdoors conditions with negligible turbulence or wind. We can witness the influence of drag for objects with exceptional aerodynamic features such as feathers and seeds of plants such as dandelions. Imagine that, in one hand, you are holding a downy feather that is about 5 cm long and weighs 10 mg. In the other hand, you are holding a round grain of quartz that also weighs 10 mg and hence is about 2 mm in diameter. When dropped from the same height in still air, the feather will float leisurely to the ground while the quartz will drop rapidly –seemingly independent of their relative weight or physical dimensions. In this example, the weight of the grain of sand is not noticeably compensated by aerodynamic traits that would allow drag to overcome the acceleration of gravity. In contrast, the slower settling time of the feather reveals the balance between gravitational acceleration and the drag caused by the feather's shape. The behavior of the feather illustrates the forces operating on small particles (particles ca. 1 to 100 μm in size) in the air. The settling speed of small particles in still air, called terminal velocity (V_s), is the constant speed of fall achieved as the increasing drag of air balances gravitational acceleration. In essence, the particles are defying gravity.

For small, smooth spherical particles, V_s can be estimated from Stokes' Law that accounts for the volumetric mass (weight/volume) and diameter of the particle and the density and viscosity of air (Gregory, 1961; Loubet *et al.*, 2007). However, microbial particles have a wide range of shapes beyond simply spherical and their surfaces are not necessarily smooth. Furthermore, their volumetric mass will depend, in part, on their state of hydration which can fluctuate. Insight into the effect of these variables on terminal velocity led scientists in the early 1900's to develop methods to directly observe the speed of fall of spores and pollen in settling chambers. Today there are several, more modern, techniques for assessing terminal velocity such as Laser Doppler Velocimetry, Particle Image Velocimetry and Time-Of-Flight particle Spectrometry (Loubet *et al.*, 2007). However, they involve expensive lasers and high-speed cameras and are not always adapted to non-spherical particles. At present, most direct observations of terminal velocity of spores, pollen and other microbial propagules involve settling chambers that are variations of the first ones deployed by Buller (1909; 1922) to observe spores of Basidiomycetes and by Yarwood and Hazen (1942) for spores of powdery mildew. These early chambers were themselves adaptations of the falling-sphere (or falling-ball) viscometers that were created after Stokes, in 1851, described the law of the non-Newtonian fall of particles through a fluid, what has become known as Stokes' Law (Cartwright, 2020).

In general, settling chambers are constructed to provide an enclosed chamber that is small enough to limit convective movement but large enough to avoid wall effects that can interfere with drag as particles settle. To build settling towers, Loubet and colleagues (2007), for example, used a 1 m section of a rectangular stainless steel tube that was 2 x 3 cm wide, Sundberg (2010) and Aylor (2002) used glass tubing of 2 cm inner diameter that was either 1.5 or 2.4 m long, and Zanatta and colleagues (2016) used a 70 cm long piece of transparent, anti-static treated PVC tubing of 24.5 cm diameter. To assure the stillness of the air and eliminate electrostatic forces, the settling chamber can be protected from the interference of electrical fields by wrapping it in aluminum foil (Gómez-Noguez *et al.*, 2017). Furthermore, the relative humidity (RH) of the air in the chamber can be regulated by humidifying the inside of the chamber

(Sawyer *et al.*, 1994). Such controls protect particles from desiccating. The stillness of the air within the chamber can be verified by introducing a puff of smoke (Aylor, 2002) and the settling times can be compared to those of certified standard microspheres (Hirose and Osada, 2016). These chambers are equipped with means to observe the falling particles and record the time required for settling. Buller, Yarwood and Hazen used a horizontal microscope and manually recorded the amount of time required for a fall over a pre-determined distance. In contrast, chambers constructed more recently are equipped with cameras with electronic shutters or with video cameras. These set-ups use various lighting techniques such as fiber optics or LEDs that avoid introducing a heat source that could cause convective movement in the chamber. The captured digitalized images can be analyzed with appropriate software thereby relieving the fastidiousness of manual notations and allowing for observation of a greater number of particles compared to what could be achieved by the early pioneers in this field. As an alternative to monitoring the settling speed of particles in a chamber, Li and colleagues (2009) placed a sliding plate at the bottom of their settling tower. The plate was marked with 1 × 1 cm grids and slid horizontally at 1 cm/sec thereby providing a record of the time of arrival of the spores in each grid. Likewise, a turning disk at the bottom of the tower can be used for the same purpose (Di-Giovanni *et al.*, 1995).

Figure 2.1 is a compilation of values for V_s reported for spores or conidia of fungi, ferns and moss and for pollen grains. The values for physical diameter on the abscissa are those reported by the authors and generally represent the diameter of a sphere of equivalent volume in cases where the propagules are not spherical. Shape factors can be calculated for non-spherical spores and are presented below. Data for spherical glass beads (volumetric mass of 2.49 g/cm^3), polystyrene microspheres (1.05 g/cm^3) and water drops (1 g/cm^3) are also indicated for comparison. The figure reveals that, overall, terminal velocity of biological propagules is roughly similar to that of water droplets and polystyrene spheres of the same physical diameter, increasing with the square of the diameter as predicted by Stokes' Law (Gregory, 1961). For most fungi and other propagules < 25 µm in diameter, V_s is < 2 cm/sec. With such slow settling speeds, a uredospore of soybean rust, for example, with V_s = 1.9 cm/sec would take almost 15 h to fall from a 1,000 m altitude in still air (Li *et al.*, 2009). If the propagules do not get caught in the battle of downward vs. upward drafts, such settling speeds indicate the strong potential for long-distance movement once they are uplifted and the challenges for these propagules to successfully deposit on new host plants. Although these data are coherent with an overall trend of increase with propagule size as mentioned above, there are striking deviations from this trend. For example, the ~3-fold variation in V_s among propagules that are ca. 9-10 µm in diameter and the 10-fold variation in propagules that are about 30 µm in diameter on Figure 2.1 are notable.

The variability of V_s among propagules of similar size but differing in other biological traits highlights how direct observations in the laboratory are particularly useful. Direct observations can account for the biological traits that influence settling speed and other aerodynamic properties. These traits are described further below. Furthermore, direct measurements can account for ambient conditions that are most pertinent to favorable epidemiological conditions. The reader should keep in mind that most of the observations reported in Figure 2.1 were made at about 20°C. At cooler, biologically relevant temperatures, for example, air would have a slightly greater density.

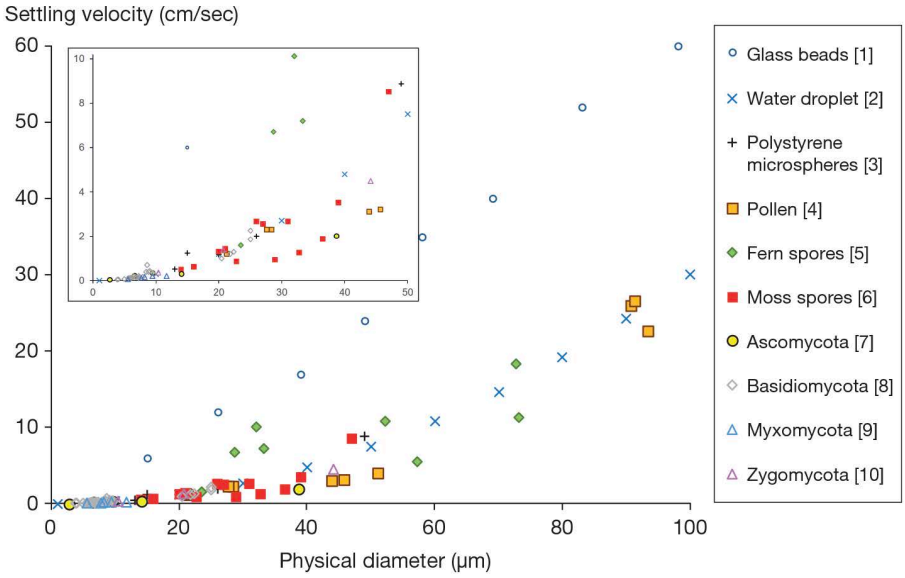


Figure 2.1. Settling velocity of various biological propagules reported in the literature based on direct measurements in settling towers compared to standard inert particles.

Settling velocities were plotted against the physical diameters reported by authors. Studies included here were those where rough approximations of equivalent diameters of spheres of equal volume were reported for the propagules. Data sources indicated in brackets in the legend are: 1: Chen and Fryrear (2001); 2: calculated based on a formula for falling water droplets derived from Stokes' Law (Gregory, 1961); 3: Sawyer *et al.*(1994); 4: corn pollen (Aylor, 2002) and pine and ragweed pollen (Hirose and Osada, 2016); 5: Gómez-Noguez *et al.* (2017); 6: sphagnum moss (Sundberg, 2010) and various other mosses (Zanatta *et al.*, 2016); 7: Mccubbin (1944) and data collected from the literature and reported in supplemental materials of Hussein and colleagues (2013); 8: Li *et al.* (2009) and Mccubbin (1944); 8 and 9: data reported in supplemental materials of Hussein and colleagues (2013); 10: Sawyer *et al.* (1994). Hemmati and colleagues (2002) also reported settling velocities for entomopathogenic zygomycetes but did not indicate specific corresponding physical diameters. The small figure inserted in the upper left corner focuses on particles < 50 µm for this same set of data.

This would slow V_s as can be seen from the details of Stokes' Law described in Chapter 4. Nevertheless, laboratory measurements have certain limitations. The propagules that are tested for settling speed are part of a population of propagules that, although they are homogenous for shape and ornamentation, have mean physical dimensions that are variable around a certain frequency distribution. Likewise, the corresponding V_s will also have a frequency distribution. For standard commercial grade *Lycopodium* spores of 35.5 µm in mean diameter, there was a Gaussian distribution of V_s with values ranging from ~2 to ~7 cm/sec for a modal value of 4.2 cm/sec and standard deviation of 0.7 (Loubet *et al.*, 2007). Similarly, for pollen from various plant species, there was also an apparent Gaussian distribution of V_s for each lot of pollen with the range of values for V_s spanning a factor of 1.4 to 2.5 depending on the plant species (Hirose and Osada, 2016). Furthermore, many microbial propagules and pollen can be emitted in the air as aggregates of numerous individual propagules. In the multiple reports summarized by Lacey (1991), aggregates of spores accounted for about 30% of the dispersal units for many different fungal species with exceptions such as *Pyrenopeziza brassicae* where 50-60% of ascospores caught in traps were in groups of four or more. It cannot be assumed that the settling speed of aggregates is linearly proportional to the dimensions

of the aggregate. There is space between the individual propagules that theoretically reduces the effective volumetric mass of the assemblage (Lacey, 1991). The aggregate can have a markedly non-spherical shape and an irregular surface. In spite of the potential irregularities of aggregates, the behavior of clusters of spores of *Uromyces phaseoli* and *Lycopodium* and pollen of *Ambrosia elator* could all be explained by the same equation: $V_{s.N} = 0.98\ V_{s.singleton}\ N^{0.53}$, where N is the number of singleton spores or pollen grains in the cluster –for clusters with up to 266 singleton components (Ferrandino and Aylor, 1984). Interestingly, this relationship was not significantly influenced by the shape of the cluster. This notion was validated on clusters that ranged in shapes where the major-to-minor axes had ratios of 1.5:1 to 3:1. However, in independent experiments, this equation over-estimated the value of V_s in 4 of 7 cases of propagule doublets (by 7 to 20%) and 5 of 6 cases of propagule triplets (by 3 to 21%) for various pollen grains and *Lycopodium* spores (Di-Giovanni *et al.*, 1995). To specifically capture propagules or aggregates according to their time of deposition, the equipment for measuring V_s that deploy sliding or turning grids at the bottom of the settling chamber, as described above, is greatly useful. It creates an archive where individual particles can be characterized therefore allowing for the various morphological and physiological factors that contribute to the variability of V_s to be considered.

⏩ Aerodynamic diameter: Rounding out the edges of physical dimensions

Another means to account for the variability of aerodynamic properties within and among species of propagules is to characterize naturally occurring propagules. These can be captured outdoors, for example, with air samplers. Air samplers draw in air under conditions where particles move throughout the sampler according to their aerodynamic properties until they reach the component part of the sampler dedicated to collection. The rate of intake of air and the trajectory of the particles in air samplers are designed to avoid premature, inertial impaction of particles on the walls of the sampler before they arrive at the collectors (Haig *et al.*, 2016). This design accounts for how particles will eventually be removed from the stream flow of the air due to i) their inertia, ii) being scrubbed from the airflow by water bubbles or iii) being moved by electrical or thermal forces. These processes are exquisitely illustrated by several different authors (Haig *et al.*, 2016; Nevalainen *et al.*, 1992). The capacity for a particle to leave a stream flow of air depends on its stopping distance. In simple terms, stopping distance is the distance a particle can travel on its own after being pushed. Stopping distance depends on the initial velocity of the particle (i.e. the air flow velocity in the sampler) and its volumetric mass and diameter (Nevalainen *et al.*, 1992). Hence, small particles can only travel relatively short distances outside of the streamflow and are less likely to experience premature impaction inside of samplers compared to larger particles. The design of samplers accounts for the distances between the streamflow of air and the collection surfaces relative to the size range of particles targeted by the sampler.

For stopping distance and V_s alike, the irregular shape of biological propagules and their varying volumetric mass complicates the notion of particle diameter. The laws of physics that describe the behavior of particles in fluids, including air, have been based on reference particles that are perfectly spherical with a volumetric mass of 1 g/cm^3 (i.e. a spherical drop of water). Irregularly shaped propagules will behave in an air stream

according to their aerodynamic diameter (D_a) –also known as aerodynamic equivalent diameter. D_a of an irregularly shaped propagule is the diameter of a spherical particle that has the volumetric mass of water and the same V_s as the propagule (Nevalainen *et al.*, 1992). Indeed, the flight of particles in moving air and their fall in still air are dependent on some of the same traits. Furthermore, the precise value of diameter to be used to calculate V_s, as described in the previous section, is D_a and not simply the physical diameter. This interrelatedness suggests a paradox where the value of one elusive variable depends on the value of another, equally elusive variable. Fortunately, as for V_s, there is specialized equipment for measuring D_a. Figure 2.2 presents a compilation of direct measurements of the D_a of biological propagules relative to estimates of their physical diameters. In contrast to the methods for direct assessment of V_s, techniques for directly assessing D_a are mostly limited to propagules with diameters less than a few 10's of microns (Mainelis, 2020). The figure illustrates examples where aerodynamic diameter deviates markedly from physical diameter. This includes spores of *Cladosporium cladosporioides* that are twice as long as they are wide with a D_a lower than expected (Reponen *et al.*, 2001) and the very elongate spores of *Alternaria brassicae* that, paradoxically, have a D_a markedly larger than expected from its physical dimensions (Mccartney *et al.*, 1993). Factors that contribute to the variability of aerodynamic properties of biological propagules are described in greater detail below.

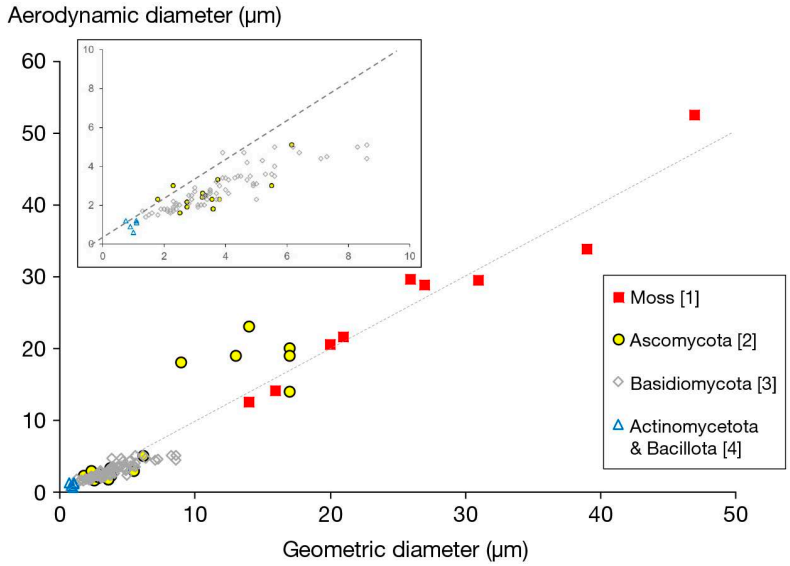


Figure 2.2. Aerodynamic diameter of biological propagules reported in the literature based on direct measurements in aerodynamic sizers compared to glass beads.

Aerodynamic diameters were plotted against the physical (geometric) diameters reported by authors. Studies included here were those where rough approximations of equivalent diameters of spheres of equal volume were reported for the propagules. Data sources indicated in brackets in the legend are: 1: Zanatta *et al.* (2016); 2: Mccartney *et al.* (1993), Reponen *et al.* (2001) and data collected from the literature and reported in supplemental materials of Hussein and colleagues (2013); 3: Hussein *et al.* (2013); 4: Reponen *et al.* (2001) and data reported in supplemental materials of Hussein and colleagues (2013). Hemmati and colleagues (2002) reported aerodynamic diameters for entomopathogenic zygomycetes but did not indicate specific corresponding geometric diameters. The small figure inserted in the upper left corner focuses on particles < 10 µm for this same set of data. The dotted line represents D_a = geometric diameter.

A comprehensive and exemplary study of the frequency abundance of aerodynamic diameters of naturally occurring biological particles in the atmosphere deployed the Ultraviolet Aerodynamic Particle Sizer (UV-APS) (Huffman *et al.*, 2010). The UV-APS measures the time it takes for a particle to travel between two laser beams after it enters the intake nozzle. D_a is calculated from the measured time of flight. The frequency distribution of particles with a D_a of up to 20 µm was assessed for air sampled at 10 m above ground on the campus of the Johannes Gutenberg University in Mainz, Germany. The differentiation of particles of biological origin from those that are inert or of mineral origin by the UV-APS is based on the natural fluorescence –at 355 nm and 420-575 nm– of reduced pyridine nucleotides (e.g., NADH and NADPH) and riboflavin, molecules that are specific to cellular metabolism. The authors detected biological particles across the entire spectrum of sizes within the limits of the UV-APS. However, the greatest abundances of biological particles were detected at D_a of about 1.5 µm, 3 µm, 5 µm, and 13 µm. A comprehensive review of >190 publications that assessed the relative abundance of bacteria and fungi of different D_a in the air –with different types of samplers– for 9 types of habitats (including outdoors) also revealed the presence of biological propagules across the full range of sizes smaller than 20 µm (Clauß, 2015). However, this compilation of results did not corroborate the peaks of abundance at the sizes indicated by Huffman and colleagues (2010). Although the UV-APS facilitates studies of dynamics of D_a of biological particles –smaller than 20 µm in diameter– its major shortcoming is the lack of information about the identity or viability of the particle. This could explain the differences in the relative abundances of sizes reported by Huffman and colleagues and those compiled by Clauß. Whatever the explanation of these differences, an important utility of measures of D_a is their contribution to estimating the expansiveness of the flight of biological propagules, especially those that are invasive species or are causal agents of disease. For this it is essential to link D_a to the specific identity of the propagule.

The Andersen (1958) sampler was designed to allow both aerodynamic sizing of biological particles, their isolation and characterization, and the quantification of their abundance. The aluminum-housed sampler is a cascade of 6 stages, each with different size cut-offs. At the ceiling of each stage, 400 holes (jets) have been drilled with successively smaller diameters, from 1.8 mm for the first stage to 0.254 mm for the sixth stage. This controls the speed of the airflow through the sampler (successively faster from the first to the sixth stage), thereby allowing particles with the appropriate stopping distance to impact on the surface of the agar in the Petri dishes positioned just below the jets. The Andersen sampler was designed to sort particles at scales according to how they might penetrate human lungs. Particles larger than about 5-10 µm are generally trapped by the nasal or oropharyngeal cavities. For smaller particles, the success of penetration deep into the lungs increases with decreasing D_a (Andersen, 1958). Hence, according to calibration with particles of carnauba wax, the D_a of the particles collected on each stage were: > 8.2 µm (stage 1), 5-10 µm (stage 2), 3-6 µm (stage 3), 2-3.5 µm (stage 4), 1-2 µm (stage 5), and < 1 µm (stage 6). Evaluation of the performance of Andersen samplers with monodisperse aerosols showed that the frequency distribution of particle size on each stage is roughly log normal (King and Mcfarland, 2012). Therefore, the mean D_a for stages 2-6 is the logarithmic midpoint of the range for each stage (with stage 1 having no upper limit).

Although the Andersen sampler facilitates identification and other characterizations of the captured propagules, the use of agar-based culture media for collection has warranted further modifications to improve sampling efficiency and the scope of the organisms that can be identified. The agar surface can cause impaction stress (and loss of viability during sampling) and particle bounce (escape of the particle from the agar surface). Both of these problems have been somewhat overcome by covering the surface of the agar in the Petri dishes (just before putting them into the sampler) with a thin layer of mineral oil (Xu *et al.*, 2013). Placing glass-fiber filters on the collection surface also greatly reduces particle bounce-off (Hu, 1971). The innovation of using glass-fiber filters for particle collection led to the development of what is referred to as non-viable Andersen cascade samplers, with 8 stages that provide more size resolution and that is adapted for chemical analyses of the captured particles. Such samplers were deployed to assess seasonal diversity of fungi according to their D_a by extracting the DNA collected on the filters of the different stages and sequencing an internal transcribed spacer that can be used for fungal identification (Yamamoto *et al.*, 2012). Samples were collected in four seasons throughout a 1-year period on the rooftop of a five-story building in New Haven, CT, USA. Basidiomycota dominated the smallest size classes of fungi (D_a of 2.1-3.3 μm and 3.3-4.7 μm) whereas Ascomycota consistently dominated the size classes where $D_a > 5.8$ μm. To identify the fungi, next generation sequencing/barcoding methods and quantitative PCR gave very similar results (Yamamoto *et al.*, 2014) thereby opening up the possibility of quantifying fungal abundance with the latter technique. Importantly, these techniques were able to highlight the genera that have a wide spectrum of D_a. For example, propagules of the *Peniphora* genus in the Basidiomycota had a high relative abundance across all D_a (from the 2.1-3.3 μm range to > 9 μm) for all four seasons (Yamamoto *et al.*, 2012). Likewise, among the Ascomycota with high relative abundance across all D_a, *Cladosporium* showed this trend for all seasons, *Mycosphaerella* in the spring and *Penicillium* in the winter. Although this approach offers more detailed biological information than the simple classification of particles as "biological" because of the presence of certain cellular metabolites, it has been limited to classification of fungi into the rather broad taxonomic groups of phyla, class and genera. However, this constraint could be overcome with molecular probes that target gene sequences used for identification of microorganisms at the species or intraspecific level.

Knowledge about the broad categories of aerodynamic diameter of airborne propagules can also be obtained from filters used for characterizing the particulate matter (PM) in the atmosphere. PM filters allow capture of coarse particles ($D_a > 2.5$ μm) that are referred to as PM_{10} particles, fine particles ($D_a < 2.5$ μm and $D_a < 0.3$ μm) that are called $PM_{2.5}$ and $PM_{0.3}$ particles, respectively, and ultrafine particles ($D_a \leq 0.1$ μm in size) called $PM_{0.1}$ particles (Ji *et al.*, 2023). Fine and ultrafine particles can penetrate into the alveoli and blood circulatory system and are linked to a range of negative effects on human health (Ji *et al.*, 2023). The use of PM filters in the study of biological propagules is usually limited to the PM_{10} and $PM_{2.5}$ categories. Furthermore, the motivation for these studies is often to understand the association of microorganisms with general particulate matter in the air (soot, dust, pollutants, etc.). Such research focuses on dusty or polluted regions where $PM_{2.5}$ content of the air surpasses the maximum acceptable levels indicated by the World Health Organization of 25 $\mu g/m^3$ (Cao *et al.*, 2014). From the perspective of human health, the association

of microorganisms with fine particulate matter can exacerbate the negative health impacts of this fine matter by adding allergens and pathogens that can penetrate into the lungs. From the perspective of microbiology, association with particulate matter can influence i) the survival of the microorganisms via either the protection offered by the particulate matter or its chemical toxicity and ii) their dissemination trajectory by altering the effective aerodynamic diameter of the propagules. In three separate studies where total $PM_{2.5}$ exceeded 200 $\mu g/m^3$ (Alghamdi *et al.*, 2014; Cao *et al.*, 2014; Yan *et al.*, 2022), bacteria, compared to fungi, dominated the microbial particles collected on both PM_{10} and $PM_{2.5}$ filters. DNA extracted from these filters was sequenced to identify the microorganisms captured. Whereas there was no significant effect of the mass or chemical composition of the particulate matter on the total concentration of bacteria or fungi (Alghamdi *et al.*, 2014), there was a significant change in the abundance of certain bacterial or fungal genera with increasing PM mass for both coarse and fine particulate matter (Yan *et al.*, 2022).

⏩ Shape, water content, ornamentation and other factors that alter aerodynamic properties of biological propagules

A hallmark of biological organisms is the expression of traits fashioned by long-term evolution that optimize survival and fitness, combined with the capacity for short-term plasticity in response to changing environmental conditions. This hallmark contributes to the variability of V_s and D_a among propagules across genera, species, etc., and also to the fluctuation of V_s and D_a among propagules of a same species or clonal group. The traits that have been shown to clearly impact aerodynamic properties of propagules include the shape of propagules, their water content and volumetric mass, and the presence of ornamentation on their surfaces.

The morphology of fungal spores and of pollen are guiding traits for identification of genera and species. Therefore, there is certain consistency of propagule shape within a taxonomic group for these organisms. Nevertheless, there can be plasticity of shape and dimensions of fungal spores in response to trophic conditions, for example. A study of ectomycorrhizal and saprophytic fungi across a gradient of resource depletion in a forest revealed that spores became more elongated for both groups and larger overall for the ectomycorrhizal fungi (Halbwachs *et al.*, 2017). This observation highlights that traits essential for aerial dissemination can be shaped by environmental factors unrelated to the dissemination process itself. Questions about the impact of shape on aerodynamic properties of fungal spores were posed in the early 1900's. Whereas the V_s of spherical particles such as the conidia of certain *Penicillium* spp., spores of mosses and many types of pollen can be rather accurately estimated from particle diameter, the settling of oblong propagules set off a debate about the physical dimension that influenced their fall. Since the experiments of Buller in the early 1900's –as described by Gregory (1961)– it has been understood that, when falling in still air, a homogenous, elongated body becomes orientated to present the maximum amount of surface in the direction of the line of fall thereby maximizing the drag. The exception observed for the fall of powdery mildew spores (Yarwood and Hazen, 1942) is likely an artefact of the experimental set-up (Gregory, 1961). The effect of non-spherical shape on V_s can be seen for the spores of sphagnum moss in Figure 2.1. These spores were described as elliptical or tetrahedral with a V_s of only 46-58% of the expected speed of a sphere of equivalent

volume and the same specific density (Sundberg, 2010). Likewise, the globular air sacs tethered to the pollen of certain pine species slowed their settling speed (Hirose and Osada, 2016) (Figure 2.1, dry pollen of ~45 μm). The plant pathologist W.A. McCubbin (1944) pursued research on the fall of asymmetrical spores because of its pertinence to the dissemination of plant pathogens. He was able to predict V_s from a mathematical function that accounted for length and width of spores. The particular cases of fusiform spores were considered as intercalated cylinders between two axial cones. However, McCubbin was not able to account for very elongated, worm-like spores such as those of *Helminthosporium sativum* that were 75 μm long and 20 μm wide. Their settling speed was only 2 cm/sec for their equivalent spherical diameter of 38 μm (Figure 2.1). This suggests that other elongated propagules such as fragments of fungal hyphae that are dispersed in the air would represent a wide range of settling velocities and aerodynamic diameters that would be challenging to estimate accurately.

Dramatic variations in shape and size of fungal propagules can also occur due to disassembling of spore masses or to disarticulation of individual spores. For example, *Monilinia vaccinii-corymbosi*, a pathogen of blueberries, produces disarticulating conidia. Conidia separate from each other during maturity but can, nevertheless, remain in chains of several conidia (Mims and Richardson, 1999). Likewise, certain members of the genus *Cordyceps*, an ascomycete with more than 600 spp. in terrestrial habitats on nearly all continents, can produce elongated disarticulating ascospores. Some species produce both disarticulating and non-disarticulating ascospores (Sung *et al.*, 2007). Spores can also be released from sporocarps as aggregates covered by a fluid that evaporates in the air leading to separation of the spores as in the case of *Ascobolus immersus* (Buller, 1909). Such dramatic changes in mass and shape of propagules are considered to be adaptations to aerial dissemination where a relatively large mass is favorable for escaping the boundary layer around the sporocarp and a relatively smaller mass favors flight in the free troposphere (Pringle *et al.*, 2016).

Water loss or uptake will influence the volumetric mass of propagules and will proportionately influence V_s according to Stokes' Law. Changes in water content can also cause swelling or collapse of propagules leading to shapes that alter aerodynamic traits. Pollen has been studied in this regard because of the natural water loss that occurs after release and during aging in the air. For corn pollen, V_s depends on the degree of hydration, ranging from 31 cm/sec for fully hydrated pollen to about 21 cm/sec for dehydrated pollen (Aylor, 2002). The change in settling velocity observed by Aylor corresponded to an increase in volumetric mass from 1.25 g/cm^3 just after collection of the pollen from the anthers to 1.45 g/cm^3 when dry, and to a concomitant change in shape from spheroid to prismatic. In contrast to pollen, some fungal spores are hygroscopic and can accumulate water during aerial dissemination depending on ambient RH. Reponen and colleagues (1996) measured the D_a of spores of fungi that are commonly inhaled into lungs such as those of species of *Aspergillus*, *Penicillium* and *Cladosporium* in an experimental set-up where the RH within the aerosol sizer was controlled. The D_a of spores of these fungi were not altered for RH in the range of 30-90%. But once the RH approached 100%, the D_a of *Cladosporium cladosporioides* increased from the initial 1.8 μm to 2.3 μm, corresponding to a doubling in overall spore size. Such increases in spore size lead to marked increases of deposition of these spores in the respiratory system.

As specified above, the application of Stokes' Law to predict the behavior of particles in air assumes that particles are smooth. Hence, rough surfaces, appendages and ornamentation on particles can influence aerodynamic behavior. A study of moss spores was able to address the influence of ornamentation on aerodynamics. Zanatta and colleague (2016) observed that V_s values for moss spores > 20 µm in diameter were generally lower than those predicted by Stokes' Law based on spore diameter. There was an increasing deviation as spore diameter increased. The authors attributed this variation to a combined effect of spore shape and ornamentation (with ornamentation being marked for some of the moss species) on the balance between volumetric mass and drag.

⏩ To what extent do aerodynamic properties matter?

As mentioned above, the main motivation for quantifying the aerodynamic properties of biological propagules is to improve the accuracy of prediction of their flight trajectories and eventual deposition, particularly as it relates to disease epidemiology and to the capacity for species to invade. Flight trajectories and plumes of deposition can be estimated with various simulation models. The particle dispersal model available from the NOAA Air Resources Laboratory[1] is a relatively user-friendly example. This model simulates plumes of deposition depending on the V_s of the particles, and therefore, it can help to address the question of how much the uncertainty of aerodynamic diameter or settling velocity really matters when predicting propagule trajectories. Based on the data compiled in Figure 2.1, microorganisms have V_s of less than 4 cm/sec and ferns and mosses can have settling velocities of about 6 cm/sec or less. Furthermore, as indicated in the previous sections, for any given species, the range of settling velocities among propagules within a population can vary by a factor of about 2 or 3. This range of V_s was used for simulations of plumes of deposition, under dry conditions, for particles emitted in major regions of wheat production in central Germany (Figure 2.3A) and southwestern Australia (Figure 2.3B). In the simulation, particles were emitted for 1 h at noon at a date in the peak of wheat harvest (see figure legend) and deposition plumes were estimated over 72 h. The simulations for the site in Germany illustrate clearly how particles of greater setting velocity deposit at shorter distances (sooner) from the source (Figure 2.3C). For this simulation, particles with V_s of 1, 2, 4 and 6 cm/sec deposited at up to 1.4, 1.2, 1 and 0.8 degrees of latitude, respectively, from the source. One degree of latitude represents about 111 km. Therefore the plumes extend from 89 to 155 km from the source. In contrast with the classical plume gradient for the simulations for the German site, the simulations for Australia illustrate unexpected outcomes when particles encounter complex air mass movements (Figure 2.3D). On the date for the Australian simulation, low altitude air masses were moving to the north with cross winds to the southeast for higher altitude air masses (based on archived data on the website of the Air Resources Laboratory). Particles with a settling velocity of 2 cm/sec were particularly affected by these cross winds. The plume of deposition extended to about the same latitude north of the source for all sizes of particles. However, for particles with V_s of 2 cm/sec, their deposition during the 72 h trajectory extended 630 km southeast from the northern-most point of the plume. In a study of the potential of microorganisms from outside of Australia to arrive on that continent via aerial dissemination, particles with D_a of 10-20 µm

1. https://www.ready.noaa.gov/HYSPLIT.php

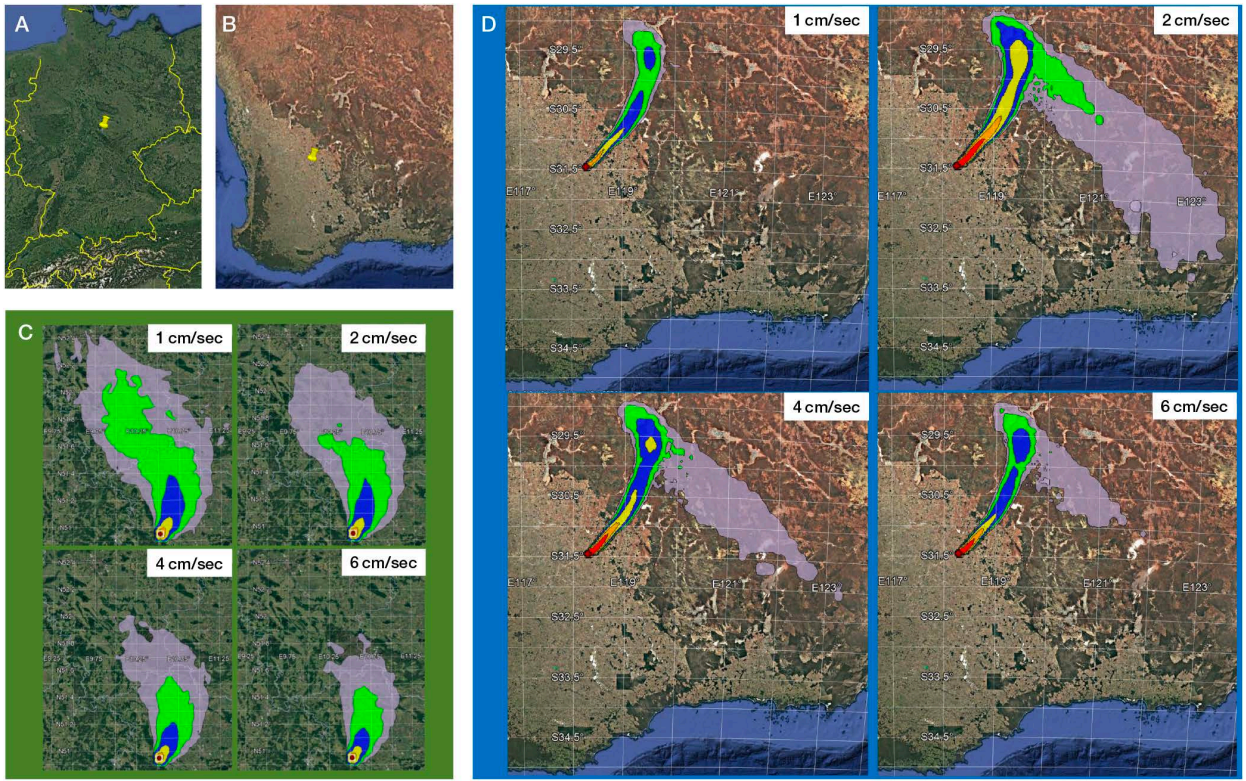


Figure 2.3. Deposition plumes for particles of different settling velocities (1-6 cm/sec) from simulations created with the dispersal model from the NOAA Air Resources Laboratory (https://www.ready.noaa.gov/HYSPLIT.php). Simulated particles were emitted for 1 h at noon in central Germany (**A**) (50.9511° N, 10.5185° E) and southwestern Australia (**B**) (31.4637° S, 118.2773° E) in the heart of major wheat production regions. Forward trajectories of plumes were simulated over a 72-h period based on archived GFS 0.25° meteorological data and archived dispersal trajectories for 15 July 2024 (for Germany, **C**) and 30 September 2023 (for Australia, **D**).

Consecutive colors from red to grey represent the decreasing relative mass of particles depositing on the ground under dry conditions. Particle deposition is relative to the 1 unit mass of particles emitted at the start of the simulation. The quantities deposited in each successive zone from red to orange to yellow to blue to green and to grey represent a 3-fold decrease in the mass deposited from the previous zone.

were considered to have the greatest potential (Wang *et al.*, 2021). Interestingly, this diameter corresponds to particles with settling velocity of about 2 cm/sec (Figure 2.1) suggesting the coherence of the simple simulation presented here with the results of previous authors. Nevertheless, the real significance of inaccurately estimating flight trajectories and plumes of deposition depends on how they miss the overlap with the contours of crops and forests, frontiers of quarantine, demographics of human population and livestock, etc.

⏩ Future challenges

The capacity for long-distance travel of biological propagules in the atmosphere has been a central question in epidemiology and invasion biology. There are multiple examples of emergences of diseases of plants, humans and animals, for example, that are the consequence of long-distance dissemination via winds (Brown and Hovmøller, 2002; Gagnevin and Pruvost, 2001; Huestis *et al.*, 2019; Sørensen *et al.*, 2000). Nevertheless, actions to manage the spread of pathogens via long-distance dissemination generally focus solely on quarantine rules about the transportation of hosts that could carry disease. The significance of long-distance aerial dissemination compared to transportation of pathogens via commercial trade has not yet been evaluated in spite of the increasing evidence of its occurrence and the numerous tools available for exploring the question. As early as 1944, McCubbin wondered about the significance of long-distance aerial spread, stating that "long-distance travel of spores must be taken into special account in plant quarantine activities because successful intercontinental transport of spores via air drifts and prevailing winds might in some cases nullify attempts to exclude for diseases by the customary port-inspection methods". These concerns have been reiterated multiple times over the decades that followed (Aylor, 1999; Davis, 1987; Schmale and Ross, 2015). Clearly, it is not possible to stop the aerial movement of microorganisms. However, accurate estimates of the extent and timing of their flight and deposition can facilitate the collection of data to validate these estimates. In practical terms it can also be of considerable service in adjusting the contours of the land cover on which these microorganisms deposit (in anticipation of their arrival) and in orienting the deployment of methods to protect hosts from succumbing to disease. By assessing the impact of long-distance aerial dissemination on disease spread relative to that of commercial transport of contaminated hosts, the financial and human resources accorded to these modes of dissemination could be adjusted accordingly.

Studies of the aerodynamics of biological propagules is dominated by questions concerning physics. However, biological processes underlie the development of the physical traits that define their aerodynamic nature. Although dissemination is the primary *raison d'être* of spores, they must also survive the voyage and germinate. Furthermore, production of propagules for dissemination is costly in terms of energy and nutrients and therefore can be in competition with vegetative or somatic growth –with consequences on the size and number of propagules produced. As mentioned above, environmental factors that are unrelated to dissemination *per se* might have consequences on aerodynamic traits via the plasticity inherent to phenotypes. In parallel, genetic variation between individuals and among nuclei within the same individual (as is common for many fungi) can produce remarkable variation in spore

sizes among offspring (Bever and Morton, 1999). An exciting challenge for the future will be to develop a broader understanding of microbial biology and evolution that accounts for the trade-offs between flight, survival and reproduction and how these trade-offs respond to the changing conditions of climate and land use.

Literature cited

Alghamdi M.A., *et al.*, 2014. Microorganisms associated particulate matter: A preliminary study. *Sci. Total Environ.*, 479-480, 109-116. https://doi.org/10.1016/j.scitotenv.2014.02.006

Andersen A.A., 1958. New sampler for the collection, sizing and enumeration of viable airborne particles. *J. Bacteriol.*, 76, 471-484. https://journals.asm.org/doi/epdf/10.1128/jb.76.5.471-484.1958

Aylor D.E., 1999. Biophysical scaling and the passive dispersal of fungus spores: Relationship to integrated pest management strategies. *Agric. For. Meteorol.*, 97 (4), 275-292. https://www.sciencedirect.com/science/article/pii/S0168192399000726

Aylor D.E., 2002. Settling speed of corn (*Zea mays*) pollen. *J. Aerosol Sci.*, 33 (11), 1601-1607. https://www.sciencedirect.com/science/article/pii/S0021850202001052

Aylor D.E., 2017. Release Mechanisms (Liberation). *In*: Aylor D.E., ed, *Aerial Dispersal of Pollen and Spores*, APS Press, St. Paul, MN, 47-69. https://doi.org/10.1094/9780890545430.004

Bever J.D., Morton J., 1999. Heritable variation and mechanisms of inheritance of spore shape within a population of *Scutellospora pellucida*, an arbuscular mycorrhizal fungus. *Am. J. Bot.*, 86 (9), 1209-1216. https://doi.org/10.2307/2656768

Brown J.K.M., Hovmøller M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science*, 297, 537-541. https://www.science.org/doi/10.1126/science.1072678

Buller A.H.R., 1909. *Researches on Fungi - Vol. I*, Longmans, London. https://doi.org/10.5962/bhl.title.4652

Buller A.H.R., 1922. *Researches on Fungi - Vol. II*, Longman, London.

Cao C., *et al.*, 2014. Inhalable microorganisms in Beijing's $PM_{2.5}$ and PM_{10} pollutants during a severe smog event. *Environ. Sci. Technol.*, 48 (3), 1499-1507. https://doi.org/10.1021/es4048472

Cartwright J.H.E., 2020. Stokes' law, viscometry, and the Stokes falling sphere clock. *Philos. Trans. R. Soc. A: Math., Phys. Eng. Sci.*, 378 (2179), 20200214. https://doi.org/10.1098/rsta.2020.0214

Chen W., Fryrear D.W., 2001. Aerodynamic and geometric diameters of airborne particles. *J. Sediment. Res.*, 71, 365-371. https://doi.org/10.1306/2dc4094a-0e47-11d7-8643000102c1865d

Clauß M., 2015. Particle size distribution of airborne micro-organisms in the environment –A review. *Landbauforsch – Appl. Agric. Forestry Res.*, https://doi.org/10.3220/LBF1444216736000

Davis J.M., 1987. Modeling the long-range transport of plant pathogens in the atmosphere. *Annu. Rev. Phytopathol.*, 25 (25), 169-188. https://www.annualreviews.org/content/journals/10.1146/annurev.py.25.090187.001125

Di-Giovanni F., *et al.*, 1995. The variability in settling velocities of some pollen and spores. *Grana*, 34 (1), 39-44. https://doi.org/10.1080/00173139509429031

Ferrandino F., Aylor D.E., 1984. Settling speed of clusters of spores. *Phytopathology*, 74, 969-972. https://www.apsnet.org/publications/phytopathology/backissues/Documents/1984Abstracts/Phyto74_969.htm

Gagnevin L., Pruvost O., 2001. Epidemiology and control of mango bacterial black spot. *Plant Disease*, 85 (9), 928-935. https://apsjournals.apsnet.org/doi/abs/10.1094/PDIS.2001.85.9.928

Gómez-Noguez F., *et al.*, 2017. Experimental measurements of terminal velocity of fern spores. *American Fern Journal*, 107 (2), 59-71. https://doi.org/10.1640/0002-8444-107.2.59

Gregory P.H., 1961. *The Microbiology of the Atmosphere*, Interscience Publishers, New York. https://doi.org/10.5962/bhl.title.7291

Haig C.W., *et al.*, 2016. Bioaerosol sampling: Sampling mechanisms, bioefficiency and field studies. *J. Hosp. Infect.*, 93 (3), 242-255. https://www.sciencedirect.com/science/article/pii/S0195670116300044

Halbwachs H., *et al.*, 2017. Mean spore size and shape in ectomycorrhizal and saprotrophic assemblages show strong responses under resource constraints. *Fungal Ecology*, 26, 59-64. https://www.sciencedirect.com/science/article/pii/S1754504816301611

Hemmati F., *et al.*, 2002. Aerodynamic diameter of conidia of *Erynia neoaphidis* and other entomophthoralean fungi. *Mycological Research*, 106 (2), 233-238. https://www.sciencedirect.com/science/article/pii/S0953756208600350

Hirose Y., Osada K., 2016. Terminal settling velocity and physical properties of pollen grains in still air. *Aerobiologia*, 32 (3), 385-394. https://doi.org/10.1007/s10453-015-9408-0

Hu J.N.H., 1971. Communication. Improved impactor for aerosol studies-modified Andersen sampler. *Environ. Sci. Technol.*, 5 (3), 251-253. https://doi.org/10.1021/es60050a003

Huestis D.L., *et al.*, 2019. Windborne long-distance migration of malaria mosquitoes in the Sahel. *Nature*, 574 (7778), 404-408. https://doi.org/10.1038/s41586-019-1622-4

Huffman J.A., *et al.*, 2010. Fluorescent biological aerosol particle concentrations and size distributions measured with an Ultraviolet Aerodynamic Particle Sizer (UV-APS) in Central Europe. *Atmos. Chem. Phys.*, 10 (7), 3215-3233. https://acp.copernicus.org/articles/10/3215/2010/

Hussein T., *et al.*, 2013. Species traits and inertial deposition of fungal spores. *J. Aerosol Sci.*, 61, 81-98. https://www.sciencedirect.com/science/article/pii/S0021850213000542

Ji X., *et al.*, 2023. Advances in particulate matter filtration: Materials, performance, and application. *Green Energy & Environment*, 8 (3), 673-697. https://www.sciencedirect.com/science/article/pii/S2468025722000632

King M.D., Mcfarland A.R., 2012. Use of an Andersen bioaerosol sampler to simultaneously provide culturable particle and culturable organism size distributions. *Aerosol Sci. Technol.*, 46 (8), 852-861. https://doi.org/10.1080/02786826.2012.669507

Lacey J., 1991. Aggregation of spores and its effect on aerodynamic behaviour. *Grana*, 30 (2), 437-445. https://doi.org/10.1080/00173139109432005

Li X., *et al.*, 2009. Estimation of soybean rust uredospore terminal velocity, dry deposition, and the wet deposition associated with rainfall. *Eur. J. Plant Pathol.*, 123 (4), 377-386. https://doi.org/10.1007/s10658-008-9374-2

Loubet B., *et al.*, 2007. A method for measuring the settling velocity distribution of large biotic particles. *Aerobiologia*, 23 (3), 159-169. https://doi.org/10.1007/s10453-007-9054-2

Mainelis G., 2020. Bioaerosol sampling: Classical approaches, advances, and perspectives. *Aerosol Sci. Technol.*, 54 (5), 496-519. https://doi.org/10.1080/02786826.2019.1671950

Mccartney H.A., *et al.*, 1993. Aerodynamic diameter of conidia of *Alternaria* species. *Plant Pathology*, 42 (2), 280-286. https://doi.org/10.1111/j.1365-3059.1993.tb01501.x

Mccubbin W.A., 1944. Relation of spore dimension to their rate of fall. *Phytopathology*, 34, 230-234.

Mims C.W., Richardson E.A., 1999. Ultrastructure of conidium and disjunctor development in the plant pathogenic fungus *Monilinia vaccinii-corymbosi*. *Mycologia*, 91, 499-509. https://doi.org/10.1080/00275514.1999.12061043

Nevalainen A., *et al.*, 1992. Performance of bioaerosol samplers: Collection characteristics and sampler design considerations. *Atmos. Environ. Part A. General Topics*, 26 (4), 531-540. https://www.sciencedirect.com/science/article/pii/096016869290166I

Pringle A., *et al.*, 2016. Reaching the wind: Boundary layer escape as a constraint on ascomycete spore dispersal. *In*: Dighton J., White J.F., eds, *The Fungal Community: its Organization and Role in the Ecosystem*, CRC Press, 309-319.

Reponen T., *et al.*, 1996. Effect of relative humidity on the aerodynamic diameter and respiratory deposition of fungal spores. *Atmos. Environ.*, 30 (23), 3967-3974. https://www.sciencedirect.com/science/article/pii/1352231096001288

Reponen T., *et al.*, 2001. Aerodynamic versus physical size of spores: Measurement and implication for respiratory deposition. *Grana*, 40 (3), 119-125. https://doi.org/10.1080/00173130152625851

Sawyer A.J., *et al.*, 1994. Dimensions, density, and settling velocity of entomophthoralean conidia: Implications for aerial dissemination of spores. *J. Invertebr. Pathol.*, 63 (1), 43-55. https://www.sciencedirect.com/science/article/pii/S0022201184710081

Schmale D.G., Ross S.D., 2015. Highways in the sky: Scales of atmospheric transport of plant pathogens. *In*: VanAlfen N.K., ed, *Annu. Rev. Phytopathol.*, 53, 591-611. https://doi.org/10.1146/annurev-phyto-080614-115942

Sørensen J.H., *et al.*, 2000. An integrated model to predict the atmospheric spread of foot-and-mouth disease virus. *Epidemiol. Infect.*, 124 (3), 577-590. https://doi.org/10.1017/S095026889900401X

Sundberg S., 2010. Size matters for violent discharge height and settling speed of *Sphagnum* spores: Important attributes for dispersal potential. *Ann. Bot.*, 105 (2), 291-300. https://doi.org/10.1093/aob/mcp288

Sung G.H., *et al.*, 2007. Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. *Stud. Mycol.*, 57, 5-59. https://doi.org/10.3114/sim.2007.57.01

Wang M.N., *et al.*, 2021. A general trait-based modelling framework for revealing patterns of airborne fungal dispersal threats to agriculture and native flora. *New Phytol.*, 232 (3), 1506-1518. https://doi.org/10.1111/nph.17659

Xu Z., *et al.*, 2013. Enhancing bioaerosol sampling by Andersen impactors using mineral-oil-spread agar plate. *PloS one*, 8 (2), e56896. https://doi.org/10.1371/journal.pone.0056896

Yamamoto N., *et al.*, 2014. Assessing the aerodynamic diameters of taxon-specific fungal bioaerosols by quantitative PCR and next-generation DNA sequencing. *J. Aerosol Sci.*, 78, 1-10. https://www.sciencedirect.com/science/article/pii/S0021850214001323

Yamamoto N., *et al.*, 2012. Particle-size distributions and seasonal diversity of allergenic and pathogenic fungi in outdoor air. *ISME J.*, 6 (10), 1801-1811. https://doi.org/10.1038/ismej.2012.30

Yan D., *et al.*, 2022. Isolation, characterization, and antimicrobial activity of bacterial and fungal representatives associated with particulate matter during haze and non-haze days. *Front. Microbiol.*, 12. https://www.frontiersin.org/journals/microbiology/articles/10.3389/fmicb.2021.793037

Yarwood C.E., Hazen W.E., 1942. Vertical orientation of powdery mildew conidia during fall. *Science*, 96, 316-317. https://www.science.org/doi/10.1126/science.96.2492.316

Zanatta F., *et al.*, 2016. Measuring spore settling velocity for an improved assessment of dispersal rates in mosses. *Ann. Bot.*, 118 (2), 197-206. https://doi.org/10.1093/aob/mcw092

Chapter 3

Approaches to quantifying emissions of bioaerosols and hunting for the hot spots

Federico Carotenuto

The first part of the journey of microorganisms in the sky involves getting into the atmosphere. The reader might wonder how they jump in, how they start this trip. The technical term is "emissions". This chapter focuses specifically on how microorganisms "take flight" and will make some mention of why that is relevant for people and for biogeochemical cycles. The reader should keep in mind that the focus of this chapter concerns the initial step of getting into the atmosphere and not on dispersal. The other chapters of the book will guide the reader through the remaining parts of this fascinating airborne trip of these astonishing travelers.

⏩ Emissions, flux and concentrations

To understand how to quantify bioaerosol emissions, we need to understand some key terminology, specifically the difference between a "flux" and a "concentration". The concentration of a given particle in the air is the amount of that particle per unit volume (e.g., 1 m^3). In contrast, a flux is the amount of the particle that crosses a given area (e.g., 1 m^2) in a given amount of time (e.g., 1 s). Therefore, this means that flux is expressed as the number of particles per square meter per second (m^2/s). We can better visualize the difference between flux and concentration if we imagine a librarian tracking the status of a book collection. From the inventory, the librarian knows that there are 1,000 books in the collection and can track the status of books in two different ways: by counting the number of books in the library each day (concentration) or by looking at the number of books that have been borrowed or returned (flux). If the librarian simply counts the books, there is no way of telling if more books go out of the library rather than are returned to the library unless the number is compared to the total inventory or to the measurements of the previous day. In contrast, the second approach tells us that information immediately. This illustrates a second important point, that flux has a direction. In mathematical terms, it means that the flux has a sign (+ or –). For micrometeorology, the convention is that positive fluxes move perpendicularly away from the surface and negative fluxes move perpendicularly toward the surface. Following this reasoning, the advantage of measuring a flux rather than a concentration of bioaerosols is obvious. The flux gives information about what's happening between a surface of interest (e.g., a grassland) and the atmosphere.

A positive bioaerosol flux represents a net emission from the surface to the atmosphere, while, conversely, a negative flux represents a net deposition of bioaerosols from the atmosphere down to the surface. Fluxes are therefore extremely useful for detecting sources and sinks of bioaerosols, and, in turn, the impact of different land-uses on emissions. Concentrations cannot be interpreted in this sense. Concentrations do not have a "direction" and are defined only by their magnitude (i.e.: they are scalar quantities). They are essentially a snapshot of the local atmospheric situation and cannot be used to identify a source or a sink unless they are paired with a modeling framework that simulates atmospheric dynamics. Depending on the averaging period and the frequency at which the concentration is measured, concentration might also be affected by long-range transport which is not representative of the immediate surroundings.

What drives these fluxes? The Earth's atmosphere is divided into different vertical layers due to variation in air temperature and density across the vertical profile. The lowermost layer of the atmosphere is the Planetary Boundary Layer (PBL), defined by Stull (1988) as "that part of the troposphere that is directly influenced by the presence of the Earth's surface and responds to surface forcings with a timescale of about an hour or less". This layer of air extends from the ground up to 2-3 km in height, with its depth varying throughout the day depending on the amount of solar energy absorbed by the Earth's surface. Mechanical and thermal effects are at play in the PBL. The mechanical effect arises from the PBL being bounded by the Earth's irregular, "rough" surface, which creates friction and generates mechanical vortices (or eddies) that influence the movement of air masses. The thermal effect results from the ground releasing the solar energy it has absorbed, which in turn generates thermally driven eddies. Eddies are vortexes of various sizes that move forward along the main wind direction and circulate the air up and down. The combination of these two effects creates a series of stochastic tri-dimensional perturbations known as "turbulence". These perturbations are due to certain parts of the flow having more kinetic energy (due to the above-mentioned mechanical and thermal inputs) than the viscosity of the fluid can absorb. These, in turn, generate abrupt changes in flow velocity that are chaotic.

The opposite of a turbulent flow is laminar flow, where the various adjacent layers of the flow move in parallel with no disruptions between them. While in a laminar flow, a bioaerosol particle would move predictably whereas the perturbations of particle movement due to turbulence are impossible to predict mathematically. Bioaerosol particles emitted from the Earth's surface are therefore subject to continuous up- and down-drafts of eddies. If the turbulence is "well-developed" and the surface keeps releasing bioaerosol particles, the eddy motions will carry, on average, more bioaerosol particles upward than down, resulting in a net positive flux (emission). This is because there is a rich source of particles close to the ground rather than up in the atmosphere. These microbial launchpads or flux hot spots are particularly interesting as they drive the atmospheric population of bioaerosols and their potential impact on atmospheric physics, as described further below.

⏩ The importance of assessing flux

Measurements of flux, as defined above, are essential for finding the association between the emissions of bioaerosols and the meteorological and surface drivers. These measurements are also the input required to model the transport of bioaerosols in the atmosphere as described in Chapter 4.

A common approach to simulating atmospheric transport is the Eulerian method, which divides the spatial domain into a 3D grid with a defined horizontal resolution covering the relevant land use and atmospheric range. The vertical grid resolution of these "cuboids" may be changed with height to capture the different dominant atmospheric scales of motion, and hence their contribution to atmospheric aerosol loads and dispersal. Within the effective surface-layer where fluxes are measured, the 3D grids may be assumed to approximate cubes in their dimensions. Within these cubes and "cuboids", Eulerian dispersal models are used to solve the following partial differential equation (Equation 3.1) as presented by Leelőssy *et al.* (2014); see also Chapter 4:

$$\frac{\delta c}{\delta t} = Q - \sum_{i=1}^{3} u_i \frac{\delta c}{\delta i} + \sum_{i=1}^{3} \frac{\delta}{\delta i}\left(K_i \frac{\delta c}{\delta i} \right)$$

While the equation seems complex, the concept it represents is relatively straightforward. In the equation, *i* ranges from 1 to 3 and represents the 3 dimensions x, y and z. The left hand term describes the variation of concentration (c) over time (t) in a cube of the model's domain, while the right hand term describes the source-reaction-deposition term (Q) and the advection of bioaerosols due to mean wind speed (u) into the corresponding three directions (x, y, z). The term to the right of the "+" sign represents the turbulence mentioned in the previous paragraph and, therefore, the transport due to turbulent motions in the three directions given the respective eddy diffusivity coefficients (K_x, K_y, K_z). Q is a summation of terms: one representing the emission of the species of interest (Q1), one representing its deposition (Q2) and one representing the time-dependent chemical reactions happening to the species in the atmosphere (Q3). In case of an inert tracer, the term Q3 is null and what remains is only emission (i.e., a positive flux) or deposition (i.e., a negative flux), so we can equate Q to the flux term "F". Equation 3.1 illustrates that the transport of bioaerosols through the atmosphere can be described by knowing essentially 3 things: the flux (F), the mean wind speed in three dimensions (u_x, u_y, u_z) and the atmospheric turbulence (K_x, K_y, K_z). Estimating F remains a key goal. Burrows *et al.* (2009) attempted to estimate it for bacteria by piecing together the existing literature and then differentiating emissions of bacteria for different land uses and ecosystems, making a first important distinction between terrestrial and oceanic areas. Oceanic fluxes were much smaller than terrestrial ones for which the overall uncertainty ranged between 80 and 870% due to the large standard deviation existing in the collated literature.

⏩ Flux measurement techniques

Given the importance of flux in the context of bioaerosol transport, one could imagine that the literature is full of these kinds of measurements. Unfortunately, that is not the case due to important measurement challenges for bioaerosol particles. For gases, the modern gold standard for flux measurement is a technique called "eddy-covariance". The technique relies on the measurement of eddies, the turbulent motions of the atmosphere mentioned above. Eddies are not all the same size. Furthermore, large eddies generate smaller ones via their own mechanical disturbance (i.e.: shear) and also generate a turbulent kinetic energy cascade towards smaller eddies. The further from the ground, the more the transport of particles through the atmosphere tends to

be assured by larger, slower, low-frequency eddies, while close to the ground smaller, faster, high-frequency eddies prevail. If we can measure the vertical velocities of these eddies at the various frequencies alongside the variation of concentration of our bioaerosols of interest, we should therefore be able to measure flux. However, eddies of all frequencies are not equally important. For flux measurement, we are generally interested in the contribution of the surface immediately surrounding us (e.g., a sunflower field or a grassland) whereas the larger, slower eddies are representative of large-scale synoptic motions beyond the surface we are measuring. The eddy covariance method separates the local contribution from the synoptic one by measuring at a very high rate (targeting the contribution of the very small and local eddies) and then averaging the high frequency data over an appropriate period to account for bigger eddies (generally between 5 minutes to 1 hour). Fluxes are then equal to the covariance between instantaneous deviations from this mean of vertical wind speed and the concentration of the scalar of interest. The formula for the eddy covariance method, as described in Equation 3.2, is:

$$F = \overline{w' c'}$$

where F is the vertical flux (in numbers per square meter per second of the scalar of interest), w' is the instantaneous deviation of vertical wind speed from the mean (meters per second) and c' is an instantaneous deviation of concentration from the mean number per cubic meter). The averaged product of the two instantaneous deviations is simply the covariance of the two variables, and therefore the flux is equal to the covariance of the turbulence (the eddies, w') and the concentration of the scalar of interest (c'). In this case both w' and s' are meant as an instantaneous deviation from a temporal mean ($\overline{w}$ and $\overline{c}$). Of course, this is a simplification of the whole method, as a series of post-processing steps are required to obtain the covariance. These steps include rotational corrections to align wind speed components to streamline coordinates, detrending to eliminate long-term drifts, etc. See Burba (2022) for an in-depth but accessible explanation.

To use the eddy-covariance method, four main assumptions must be met (Foken *et al.*, 2012):

– Both variation in concentration and in three-dimensional wind speed are measured fast enough to resolve high frequency eddies (i.e., 10-20 times per second).

– Air density fluctuations must be accounted for. It is usually possible to take into account density fluctuations by combining measurements over flat terrain with no significant orography and when applying opportune mathematical corrections to flux data (Webb *et al.*, 1980).

– Mean vertical wind speed (i.e., $\overline{w}$) is negligible, so that no flow divergence or convergence occur, as is generally the case for horizontally homogeneous terrain.

– The surface source (or sink) strength can be approximated by the vertical eddy covariance term. This means that the horizontal eddy terms are negligible. This generally happens during the daytime when there is vigorous vertical mixing. During nighttime cooling, the surface layer becomes often stratified and vertical motions are very limited. In this situation, the Eddy-Covariance technique cannot be applied.

The notion of "fast enough" in assumption #1 is at the heart of the difficulty of measuring the flux of bioaerosols. This refers to the response time of the sensor –rapid enough to detect fast changes in wind speed and concentration. A slow

response sensor, even when polled (or queried) at 20 Hz, will not be able to resolve atmospheric turbulence. Time response is how fast data updates; polling frequency is how often the data are checked. Like watching a soccer game with a camera that updates once per minute –no matter how often you look– you will miss the action. However, with a fast camera snapping 20 frames per second, each check reveals real-time changes.

In light of these assumptions, it might seem straightforward to measure fluxes of bioaerosols with the eddy covariance technique on flat homogeneous surfaces such as grasslands, croplands, forests, etc. However, this has never been achieved. Detection of rapid changes in concentrations of bioaerosols is the obstacle. Whereas it is possible to detect small variations in concentrations of wind speed (via ultrasonic sensors) and gases (CO_2 and CH_4 through optical sensors measuring the absorption of certain infrared wavelengths) in 0.1 second, no equivalent technology can reliably do this for bioaerosols.

The few studies that attempted to measure a bioaerosol flux have used the "gradient method" approach that was widely deployed in the past when fast sensors did not exist at all. Today it is still used when it is not possible to measure "fast" fluctuations in concentrations. In this approach, the difference in concentration between two heights (measured with slow classical sensors) is then scaled to a flux via different parameterizations. These latter parameterizations might vary; certain projects used a function of wind speed that worked well with saltating dust (Lindemann *et al.*, 1982; Lindemann and Upper, 1985), other used fast measurements of turbulence and temperature assuming that they provide a description of the surface layer's profile (Lighthart and Shaffer, 1994). Gradient methods, though, tend to be challenging. Instruments need to be quite precise (or well cross-calibrated) to make sure that the difference in concentration in the vertical profile is due to the presence of a real gradient, rather than a systematic bias due to constant difference in measuring bioaerosols' magnitude. This often translates into a minimum resolvable gradient, below which only noise is detectable. This minimum resolvable gradient dictates that the instruments might need to be placed at significant height difference between one another. Gradient methods are not always applicable where there is a significant canopy (such as with a forest). The larger eddies generating the turbulence and atmospheric profiles on which the gradient method is rooted, break down when encountering a significant canopy. Furthermore, there are often large-scale incursions of fast-moving air without a clear pattern. For these reasons, the gradient method fails below a canopy. Furthermore, the gradient method is not a direct measurement of a flux and might be quite labor intensive, depending on how the concentration of bioaerosols is measured. This is the second crucial difference between the measurements of a flux for a trace gas such as CO_2 versus bioaerosols. For CO_2, the concentration is unambiguous, expressed as moles of gas per cubic meter of dry air. The concentration of bioaerosol is not so easily defined. This could be the amount of total culturable microorganisms, of pollen grains, of epifluorescent particles, etc. per cubic meter of air. For example, Lindemann *et al.* (1982) and Crawford *et al.* (2014) both used a gradient method with the same parameterization approach, but Lindemann and colleagues counted culturable bacteria over croplands whereas Crawford and colleagues counted the number of fluorescent particles as measured by an ultraviolet light-induced fluorescence spectrometer over a

forest. Numbers for Lindemann *et al.* ranged between 57-543 colony forming units (CFU)/m^2/s, while for Crawford and co-authors between 0 and >2,000 fluorescent bacterial-like particles/m^2/s. While the orders of magnitude are quite similar, it is difficult to pinpoint the causes of this difference. Is it only due to the different ecosystems or to the different enumeration techniques? These difficulties illustrate why the uncertainty of Q from the previous section is large.

Figure 3.1 summarizes the different approaches to flux measurements. The distinction between the approaches concerns the time response of the instrument for measuring the bioaerosol concentration and whether there is a non-real-time response to bioaerosol concentrations or a (quasi-)real-time response of the instrument used as described below.

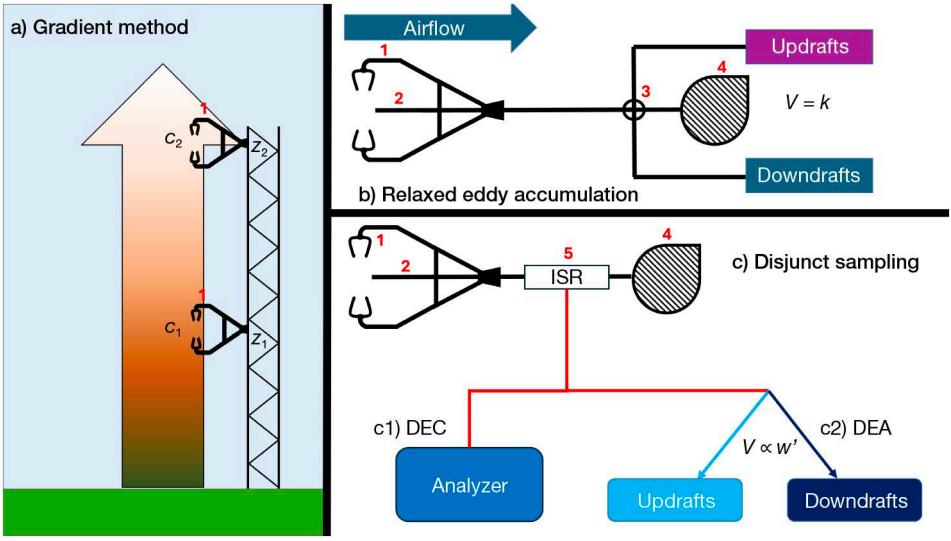


Figure 3.1. An overview of the various approaches to flux measurement.

Gradient method (**a**), Relaxed Eddy Accumulation (**b**), and Disjunct sampling methods (**c**). Numbers in red indicate key parts of the systems. Instruments #1 are sonic anemometer-thermometers for fast measurements of wind speed and temperature, # 2 are inlets, #3 is a fast-switching valve used in REA to select the reservoir, #4 is a pump passing air through the system and #5 is the so called "Intermediate Storage Reservoir" that is sampled very quickly. The air in the ISR is then passed to either an analyzer (DEC) or reservoirs for updraft and downdraft as per REA (DEA). For DEA the amount of passed air is proportional to the turbulent vertical wind speed whereas in REA a constant flowrate is used. In a, instead, z1 and z2 represent the two heights of sampling and c1 and c2 the concentrations measured at those height with any kind of sampler. In illustration "a", instruments are represented as sonic anemometers as sensors that can measure both wind speed and air temperature. However, in reality, the technique would require either a single 3D sonic anemometer at the top to derive turbulence information or two (or more) 2D sonic anemometers and thermocouples to derive the wind speed and temperature profile. DEA, Disjunct Eddy Accumulation; DEC, Disjunct Eddy Covariance; ISR, Intermediate Storage Reservoir; REA, Relaxed Eddy Accumulation.

Non-Real-Time Response Approaches

These involve measurements that do not immediately yield information about concentration during sampling such as counting of microbial colonies on culture

medium, epifluorescence microscopy, and DNA extraction. For these approaches, only the gradient method is realistically applicable given the current available technologies. While different aerobiology studies used different approaches to scale the concentration gradient to a flux (e.g., Lindemann *et al.*, 1982; Lighthart and Shaffer, 1994), the approach based on the Monin-Obukhov Similarity Theory (MOST, Monin and Obukhov, 1954) is the one which received the greatest amount of validation from the micrometeorological community (Businger *et al.*, 1971; Kaimal *et al.*, 1976). It is still used and is being expanded (e.g., Stiperski and Calaf, 2023). MOST relies on the fact that in the lower layer of the atmosphere in contact with the ground, the vertical profiles of wind speed, temperature and scalar concentrations are linked with the fluxes. Therefore, it is possible to infer the flux from a gradient given the appropriate so-called similarity function. Briefly, MOST requires measuring a gradient of concentration at two or more heights within the surface layer. But while the surface layer can be hundreds of meters deep, gradients are generally stronger close to the ground where we are closer to the emitting/absorbing surfaces (e.g., plant leaves). As mentioned previously, surface elements contribute to mechanical turbulence as they interact with the moving air masses. In the layer of air in contact with these so called "roughness elements" (blades of grass in a grassland, trees in a forest, etc.), MOST fails as the profile is disturbed by the interaction with the surface itself. The lowermost point in the gradient should be above this disturbed layer of air (called the "roughness sublayer"). The height of this layer depends on the height of the roughness elements, and it will be practically inexistent on smooth flat surfaces such as lakes and deeper when the roughness elements are significant such as in forests or cities. To scale this gradient to a flux, it is either necessary to measure a profile of wind speed and air temperature, or to derive turbulence quantities directly via the deployment of a sonic anemometer at the topmost height of sampling. Carotenuto *et al.* (2017) used a sonic anemometer to infer fluxes of total culturable microorganisms over a grassland. In addition to the previously mentioned restrictions and the need to measure within the surface layer, the gradient method requires flat and homogeneous terrain to avoid local boundaries that are not representative of the overall environment being measured. In addition, MOST similarity corrections are adapted to unstable and stable atmospheres.

A significant technical investment could overcome the limitations regarding flat homogeneous terrain and the need for a significant height difference between the sampling points. Brunet *et al.* (2013) and Wéry *et al.* (2017) have suggested employing the Relaxed Eddy Accumulation (REA) method in aerobiology. In this method, turbulence is measured as per the eddy covariance method. Air is sampled at a constant flow rate but is directed to different reservoirs depending if the vertical wind velocity is upward ($w'>0$) or downward ($w'<0$). The reservoir accumulates particles for a certain duration (e.g., 30-60 minutes) and then the contents are analyzed off-line in the laboratory as per the gradient method above. The flux for that period is then the product of i) a coefficient dependent on the acquisition conditions, ii) the standard deviation of the vertical wind velocity and iii) the difference in concentrations between the reservoirs (Fotiadi *et al.*, 2005). There is still no commercial system for bioaerosol REA given challenges of fast-switching valves and maintaining constant flowrate sampling without losses. Table 3.1 provides an overview of magnitude for bioaerosol fluxes measured with the gradient method.

Table 3.1. Examples of bioaerosol fluxes measured with the gradient method.

Reference	Aerosol type	Surface	Sampling	Flux	Units
Lindemann *et al.* (1982)	Bacteria	Winter Wheat	Impaction	+57	CFU/m^2/s
Lindemann *et al.* (1982)	Bacteria	Bean	Impaction	+499	CFU/m^2/s
Lindemann *et al.* (1982)	Bacteria	Bare Soil	Impaction	+124	CFU/m^2/s
Lindemann *et al.* (1982)	Bacteria	Alfalfa	Impaction	+543	CFU/m^2/s
Lindemann and Upper (1985)	Bacteria	Bean	Impaction	+33.8 - +211.5	CFU/m^2/s
Lighthart and Shaffer (1994)	Bacteria	Chaparral	Impaction	<0 - +4.67	CFU/m^2/s
Crawford *et al.* (2014)	Bacteria (Wet)*	Pine Forest	Optical*	≈-2,000 - +2,000	#*/m^2/s
Crawford *et al.* (2014)	Bacteria (Dry)*	Pine Forest	Optical*	≈ 0 - +2,000	#*/m^2/s
Crawford *et al.* (2014)	Fungi (Wet)*	Pine Forest	Optical*	≈-6,000 - +4,000	#*/m^2/s[1]
Crawford *et al.* (2014)	Fungi (Dry)*	Pine Forest	Optical*	≈ -2,000 - +2,000	#*/m^2/s
Carotenuto *et al.* (2017)	Total cultivable	Grassland	Virtual Impaction	-5.2 - +57.1	CFU/m^2/s

* In Crawford *et al.* (2014) aerosol type is inferred by a light-induced fluorescence spectrometer, and therefore the aerosol type must be considered broadly as bacteria- or fungi-like.

(Quasi-)Real-Time Response Approaches.

In the past 10 years new instrumentation became commercially available relying on laser/light induced fluorescence (LIF) to quantify airborne bioaerosol concentrations. These instruments use fast optical measurements where each particle entering the sampling chamber is excited by a filtered xenon flashlamp, LED or a laser at a given wavelength. The resulting fluorescence spectrum (autofluorescence) is measured by the instrument's detector. Stronger fluorescence signals are expected from particles that contain organic compounds such as tryptophan and NADH, typical of biological particles such as bacteria, fungi and eucaryotic cells. Huffman *et al.* (2020) gives an in-depth review of these kinds of instrumentation and their limitations. In short, LIF spectrometers can distinguish between biological and non-biological particles (albeit with limited specificity and with certain margins of error) and can achieve the measurements in real-time, as soon as each particle traverses the measurement chamber. While their time response is not enough for a direct application of the eddy-covariance (EC) method, it is fast enough to potentially extend their application beyond the gradient and the REA methods. One alternate method called disjunct eddy covariance (DEC; Rinne *et al.* 2001) is a variation of the EC method based on the possibility of taking only a subset of samples from the high-frequency time series of wind speed and

concentrations that the EC method measures. If sampled in a specific way, this subset of data, albeit "disjunct", will be enough to compute a flux which is equal to the flux computed by EC with only minor random differences. DEC is no small technical feat; to be representative, air needs to be sampled in the reservoir in less than one second and the downstream analyzer should be able to handle the sample passed from the reservoir in 1-30 seconds (Turnipseed *et al.*, 2009). If our analyzer is slower than this, there is still the possibility to use disjunct sampling by passing the sampled air to two separate reservoirs as per REA. The only difference is that, thanks to the discrete sampling approach, the volume of air passed to the upward and downward reservoir will be proportional to the vertical wind velocity. This eliminates the need for the "relaxation" part of REA that forced the method to sample in the two reservoirs with a constant flowrate and is, in fact, a Disjunct Eddy-Accumulation (DEA) method. Turnipseed *et al.* (2009) tested both DEC and DEA on CO_2 fluxes alongside traditional EC measurements and concluded that, even though the fluxes exhibited good agreement, there was a large uncertainty (around 40%) because of the reduction in statistical sampling (due to the disjunct collection) and the precision of the analytical instrument employed in the study. Turnipseed *et al.* (2009) worked on gases, which are surely different from bioaerosols, but if similar uncertainties could be reached also for bioaerosols, it would still be a major improvement, considering the uncertainties calculated by Burrows *et al.* (2009). The method, however, requires significant technical efforts to properly synchronize all the involved valves and instruments and to be able to sample quickly enough a volume of air that is sufficiently full of biological particles to be detectable by the downstream instrument. Technical issues will arise also regarding the definition of a correct sampling head and inlet to minimize losses and interference with the sonic anemometer as well as addressing issues in flowrate and saturation of particles in the sensor. Still, previous attempts at sampling inorganic dust can yield precious insights on how to face these problems (Fratini *et al.*, 2007; Dupont *et al.*, 2021).

⏩ Modeling fluxes and hunting for hot spots

Once a method of measuring bioaerosol flux is chosen, we need to deal with the questions of where to measure and how to upscale. In essence, how can values of Q be obtained for each grid-box of a regional –or planetary– model? One answer has been proposed by Carotenuto *et al.* (2017). The PLant-Atmosphere Epiphytic Transport (PLAnET) model simulates the variation in both the epiphytic and atmospheric concentrations of microorganisms, and their removal and deposition on the underlying land cover and yields a net flux of microorganisms between the plant canopy and the atmosphere. Briefly, in PLAnET the gross upward flux of microbes from the plant canopy is modeled as a function of friction velocity (u_*) and the ratio between the current population of microorganisms in the phyllosphere (i.e., on leaves and other aerial plant parts) and the ecosystem carrying capacity –with some biophysical scaling for the particles involved. Friction velocity is a surface layer scale velocity related to surface drag. In other words, it is a measure of mechanical turbulence due to wind shear and is therefore already an indicator of local turbulence. Using u_* to model flux is not new: dust saltation models assume that there is either a linear (Raupach and Lu, 2004) or exponential (Gillette and Passi, 1988) relationship between friction velocity and upward dust flux due to the existence of saltation bombardment (Raupach and Lu, 2004; Dupont *et al.*, 2013). Saltation bombardment is a mechanism through which

coarser dust particles saltate on the ground releasing finer dust particles that are then uplifted by turbulence (Alfaro *et al.*, 2022). The main difference is that for microorganisms it's hard to imagine a saltation approach. Therefore, in PLAnET, it is assumed that the upward flux will tend to saturate at a certain friction velocity in the absence of a mechanism amplifying the ejection from the phyllosphere (i.e., saltation). Furthermore, in PLAnET it is considered that a certain fraction of the population will always remain sheltered from the action of the wind following the experiments of Waggoner (1973). Technical differences notwithstanding, the concept remains similar between upward fluxes of dust and microorganisms: wind shear stress contributes to their removal from the surface. Nevertheless, Alfaro *et al.* (2022) noticed an effect of the stability of the surface layer on dust fluxes, namely that at similar values of friction velocity there are more grains participating in saltation in unstable versus quasi-neutral stratification. This reconnects with our description of the PBL made in the first paragraph, which mentioned two forces acting on the turbulence, one mechanical (u_*) and one thermal due to incoming solar radiation. Depending on the type of surface, a certain amount of the incoming radiation is expended to convert liquid water into water vapor (latent heat flux) and part of it directly contributes to the atmospheric turbulence (sensible heat flux, H). H and u_* are the two physical variables that contribute to turbulence and, therefore, to atmospheric stability. The results of Alfaro *et al.* (2022) seem to indicate that for dust fluxes the thermal forces are also important. These two variables are related to one another by a third parameter, the Richardson flux number (R_{if}, e.g., Katul *et al.*, 2014). The more R_{if} is negative the more unstable the atmosphere becomes, and turbulence grows more intense. Positive numbers indicate a stable atmosphere (inhibiting turbulence), while R_{if}s close to 0 represent a neutral atmosphere where the thermal and mechanical contributions to turbulence are balanced. Besides H and u_*, the Richardson flux number is also a function of air temperature and the gradient of wind over a certain height, as described in Equation 3.3:

$$R_{if} = \frac{\left(\frac{g}{T}\right)\frac{H}{\rho C_p}}{-u_*^2\left(\frac{dU}{dz}\right)}$$

where g is the acceleration of gravity (in m/s^2), T is the air temperature (in K), H is the sensible heat flux (in W/m^2), ρ is air density (in kg/m^3), C_p is air specific heat capacity (in J/kg/K), u_* the friction velocity (in m/s), U is wind speed (in m/s) and dz is the height across which the wind speed gradient is calculated (in m).

All of these variables work across scales, from fields to continents, and are available across the planet and at an hourly resolution thanks to meteorological forecasts and meteorological reanalysis such as the European Center for Medium-range Weather Forecast (ECMWF) Reanalysis v5 (ERA5, Hersbach *et al.*, 2020). ERA5 and its derivates are products of the Copernicus Climate Change Service (C3S) at the ECMWF and use state-of-the-art numerical weather models to assimilate multiple observations from various sources and give the best possible representation of the Earth's atmosphere and surface processes from roughly 1950 to the present. Figure 3.2 shows a snapshot of R_{if} computed for a European spatial domain at 12:00 UTC on the 17th of July 2024 –in other words a Richardson number map.

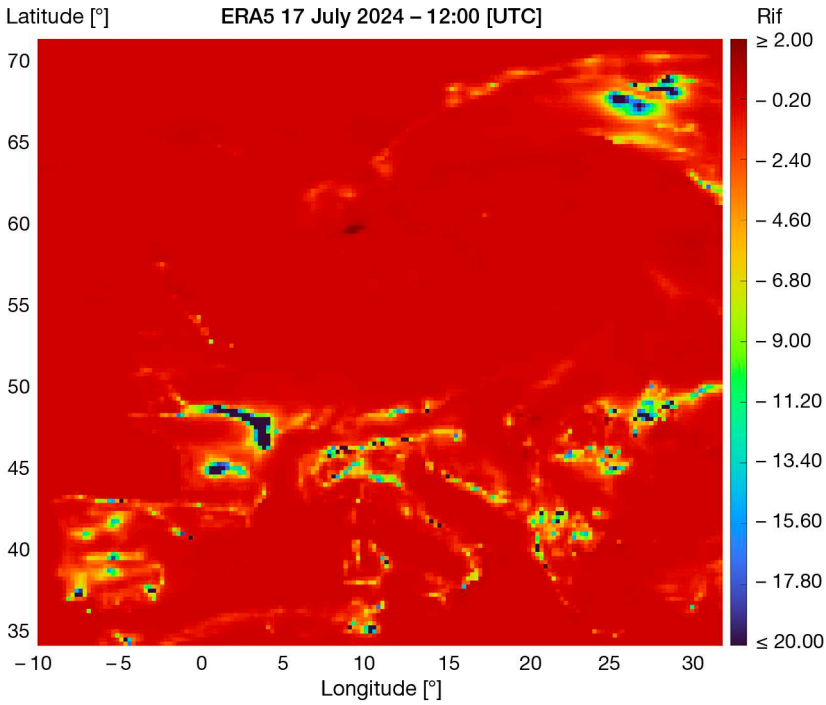


Figure 3.2. Map of R_{if} as computed by a combination of ERA5 u_*, H, air temperature and wind speed at 10 m for 12:00 UTC on 17 July 2024. The values of g and ρC_p have been considered constant and equal to 9.8 m/s^2 and 1.21 e^3 J/kg/K.

Beyond illustrating a generalized atmospheric instability, the figure does not clearly highlight hot spots except some small areas mostly located over significant orography. PLAnET, whilst making use of u* to derive upward fluxes, also takes into account a simulated surface concentration scaled by the ecosystem carrying capacity. This is because turbulence alone is not enough to generate an emission. A certain amount of the scalar to be transported must be available. In the absence of a source (or in the case of an active sink, such as the sea, see Mayol *et al.*, 2014) turbulence will mostly deposit bioaerosols that were already airborne toward the surface, resulting in a net negative flux. Therefore, the next step is to map the potential sources of bioaerosols in order to mask out the areas that are not expected to contribute to the emission of microorganisms from plant canopies. Given our focus on vegetation here, it would be useful to have an equivalent of Rif for plant canopies. Fortunately, there is something similar thanks to the advances in remote sensing and Earth observation. The Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Terra and Aqua NASA satellites takes snapshots of Earth's surface every 1 to 2 days at multiple wavelengths, including in the red and in the Near Infra-Red (NIR). Given that vegetation strongly absorbs red light and strongly reflects NIR, it is possible to leverage this spectral difference to build an index. The Normalized Difference Vegetation Index (NDVI) is a ratio between bands in the red and NIR and ranges between –1 and 1 having the highest values for actively photosynthesizing vegetation (Myneni *et al.*, 1995). NDVI values close to 0 generally indicate bare soils, while values <0 are found over water.

Considering that the ERA5 resolution is 0.25° x 0.25°, the MODIS 0.05° 16-days NDVI (Didan, 2021) is the best option to overlay an estimate of sources to the Rif map of Figure 3.2 by choosing a threshold above which a MODIS pixel can be identified as green photosynthetic vegetation (for this example, >0.25 NDVI). Finally, mountains are generally more turbulent areas as their elevation makes them a roughness element of the surface interfering with wind circulation potentially increasing wind shear or decreasing static stability (Bougeault and Lacarrere, 1989). As a final step we can then use a Digital Elevation Model (DEM) to mask all the places with significant elevation (for this example, >1,500 m) from our map. The ETOPO1, 1 arc-minute resolution global relief model (NOAA, 2009; Amante and Eakins, 2009) from the USA National Oceanographic and Atmospheric Administration (NOAA), has been used for this final step given the relatively coarse resolution of the ERA5 data. Figure 3.3 shows the MODIS and DEM datasets (harmonized to ERA5 resolution) and the resulting map of masked Rif.

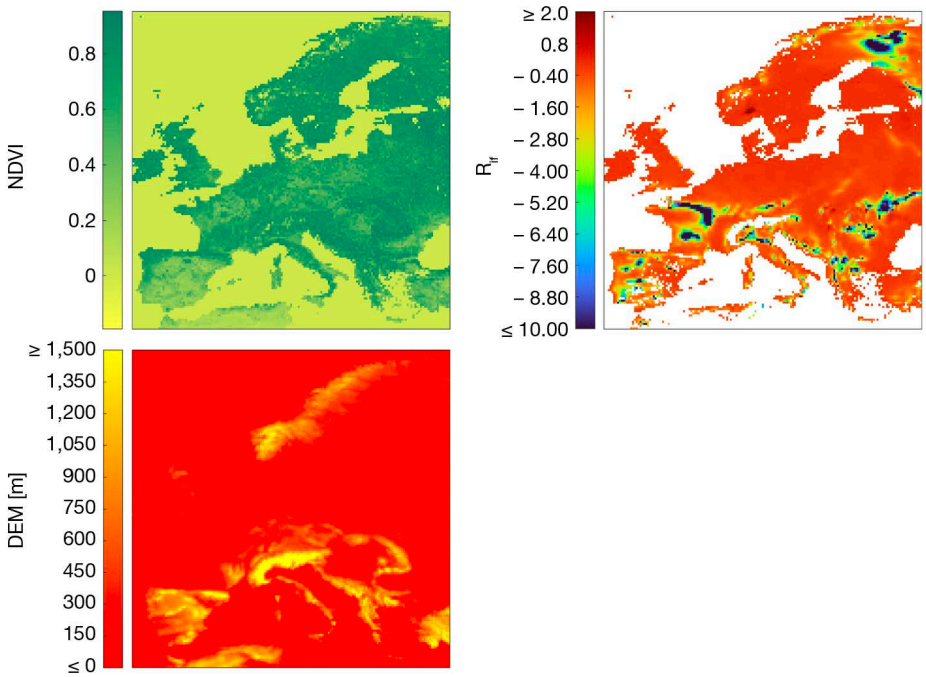


Figure 3.3. Maps of NDVI (left), DEM (center) and R_{if} (right) after applying NDVI and DEM masks. Note that the R_{if} scale has been changed from that in Figure 3.2 to enhance the visualization after applying the masks.

NDVI, Normalized Difference Vegetation Index; DEM, Digital Elevation Model.

The rightmost plot in Figure 3.3 shows the R_{if} map "cleaned" of non-vegetated pixels and orographic effects. The bluer spots are those where the atmosphere is highly unstable and therefore prone to turbulent motions. This is far from saying that those are the spots where bioaerosols fluxes should be sampled, but it illustrates a method, coherent with flux sampling and emission models such as PLAnET, to hunt for hot spots that could yield significant emission fluxes. This approach, for example, could

be applied to a long time-series of hourly data and the frequencies of R_{if}s conductive to turbulence analyzed to highlight consistent hot spots. PLAnET has been calibrated and validated only on a grassland ecosystem and would need more measurements over different surfaces to iterate on its structure and its coefficients to be reliably usable over the whole biosphere. Identifying putative hot-spots –and cold spots– could help achieve this by fostering improvement of parameterization in PLAnET as well as the birth of new bioaerosol emissions models. Identification of hot-spots would also involve understanding sources in terms of quality and quantity. Specifically, knowledge of sources of biological ice nucleators (such as *Pseudomonas syringae* or rust fungi) involved in the bioprecipitation cycle can improve understanding of how vegetated landscapes influence the water cycle (Morris *et al.,* 2014; Moore *et al.*, 2021). In summary, hot spots are not a goal in themselves, but rather are a means to improve model parameterization and insight into bioaerosol dynamics. Upscaling and transferring PLAnET emissions to global transport and circulation models is, of course, not straightforward. PLAnET is non-dimensional by design: the spatialization of its emissions depend on the grid-size of the input data. As for the example of ERA5 above, many global circulation models work at a very coarse space resolution (0.25° are roughly 28 km at the Equator) in comparison with the ground sampling that can realistically be accomplished in light of the small footprint (a few hundred meters) of the REA, DEA and DEC measurement methods. This introduces uncertainty when attempting to upscale high-resolution data to a low-resolution spatial grid. This is generally solved by downscaling input meteorological data to a resolution that is more coherent with the physical phenomena to be simulated. Downscaling approaches generally fall into two categories: statistical and dynamical (de Lima Morales and Motlagh, 2024). The statistical approach relies in establishing relationships between coarse variables and finer-scale data from a limited set of observations. Dynamical downscaling relies on running regional (or local) circulation models that, by taking coarse data as input, produce a downscaled dataset by simulating all the appropriated physical dynamics. However, while simpler statistical models might have issues in extrapolating the downscaling relationship when there is a lack of appropriate observations, dynamical models are quite computationally intensive. More advanced statistical methods, such as machine learning techniques, might improve downscaling capabilities and cut down on computational cost, especially when dealing with the simulation of future scenarios (Lin *et al.*, 2023; Jimenez *et al.*, 2024; de Lima Morales and Motlagh, 2024). A final step is then required for establishing the appropriate feedbacks: the combination of an appropriate grid of emissions as simulated by the PLAnET model which feeds a circulation and transport model is not enough. Bacteria, for example, are not passive tracers since they can interact with clouds and affect precipitation. This should, in turn, affect our emissions estimates as precipitation might trigger further release of microorganisms (e.g., Crawford *et al.*, 2014) which means that feedback mechanisms must be included in the models to be able to evaluate the effect of microorganisms both in the atmosphere and on the surface (and on themselves!).

The application of PLAnET on a global scale, or any other model capable of relating proxy variables from easily accessible databases to bioaerosols fluxes, would not limit its usefulness to the validation of scientific hypotheses. Being able to simulate a new surface-to-atmosphere feedback would mean better weather forecast models as well as a better simulation of future scenarios related to climate change. It would also

shed light on potential source-receptor connections, meaning that surface alterations such as land-use changes in one place, could then impact distance areas via long-range transport (Creamean *et al.*, 2013; Francis *et al.*, 2022). While PLAnET is geared towards microorganisms in the plant canopy, similar principles could be applied to simulate emissions of human pathogens that are also expected to be impacted by climate change (Mora *et al.*, 2022). In short, there are societal and political benefits to simulating the emissions and dispersal of bioaerosols with minimal uncertainty. With the construction of digital twins of the whole Earth system (Bauer *et al.*, 2021) being carried out by both public[2] and private agents[3], introducing the feedback between surface, atmosphere and humans mediated by bioaerosols would allow for unprecedented simulations of multiple scenarios that could help us to best address the environmental issues that we are facing.

⏩ Literature cited

Alfaro S.C., *et al.*, 2022. Unraveling the roles of saltation bombardment and atmospheric instability on magnitude and size distribution of dust emission fluxes: Lessons from the JADE and WIND-O-V experiments. *J. Geophys. Res.-Atmos.*, 127 (12), e2021JD035983. https://doi.org/10.1029/2021JD035983

Amante C., Eakins B.W., 2009. ETOPO1 1 arc-minute global relief model: Procedures, data sources and analysis, Technical Memorandum NESDIS NGDC-24, National Geophysical Data Center, NOAA, 25 p.

Bauer P., *et al.*, 2021. A digital twin of Earth for the green transition. *Nat. Clim. Change*, 11 (2), 80–83 https://doi.org/10.1038/s41558-021-00986-y

Bougeault P., Lacarrere P., 1989. Parameterization of orography-induced turbulence in a mesobeta-scale model. *Mon. Weather Rev.*, 117 (8), 1872-1890. https://doi.org/10.1175/1520-0493(1989)117<1872:POOITI>2.0.CO;2

Brunet Y., *et al.*, 2013. A relaxed-eddy accumulation system for measuring microbial emission fluxes from the vegetation. 32nd American Association for Aerosol Research Annual Conference, Portland, Oregon, USA.

Burba G., 2022. *Eddy Covariance Method for Scientific, Regulatory, and Commercial Applications*, LI-COR, https://www.licor.com/env/products/eddy-covariance/ec-book/

Burrows S.M., *et al.*, 2009. Bacteria in the global atmosphere – Part 1: Review and synthesis of literature data for different ecosystems. *Atmos. Chem. Phys.*, 9 (23), 9263-9280. https://doi.org/10.5194/acp-9-9263-2009

Businger J.A., *et al.*, 1971. Flux-Profile Relationships in the Atmospheric Surface Layer. *J. Atmos. Sci.*, 28 (2), 181-189. https://doi.org/10.1175/1520-0469(1971)028<0181:FPRITA>2.0.CO;2

Carotenuto F., *et al.*, 2017. Measurements and modeling of surface-atmosphere exchange of microorganisms in Mediterranean grassland. *Atmos. Chem. Phys.*, 17 (24), 14919-14936. https://doi.org/10.5194/acp-17-14919-2017

Crawford I., *et al.*, 2014. Characterisation of bioaerosol emissions from a Colorado pine forest: Results from the BEACHON-RoMBAS experiment. *Atmos. Chem. Phys.*, 14 (16), 8559-8578. https://doi.org/10.5194/acp-14-8559-2014

Creamean J.M., *et al.*, 2013. Dust and biological aerosols from the Sahara and Asia influence precipitation in the Western U.S. *Science*, 339 (6127), 1572-1578. https://doi.org/10.1126/science.1227279

de Lima Moraes A.G., Khoshnood Motlagh S., 2024. The climate data for adaptation and vulnerability assessments and the spatial interactions downscaling method. *Sci. Data*, 11 (1), 1157. https://doi.org/10.1038/s41597-024-03995-6

2. Destination Earth, from the European Commission: https://destination-earth.eu/; Earth System Digital Twin, from NASA: https://esto.nasa.gov/earth-system-digital-twin/

3. Earth-2, from NVIDIA: https://www.nvidia.com/en-us/high-performance-computing/earth-2/

Didan K., 2021. MODIS/Terra Vegetation Indices 16-Day L3 Global 0.05Deg CMG V061. *In*: NASA EOSDIS Land Processes Distributed Active Archive Center, https://doi.org/10.5067/MODIS/MOD13C1.061

Dupont S., *et al*., 2013. Modeling saltation intermittency. *J. Geophys. Res. Atmos.*, 118 (13), 7109-7128. https://doi.org/10.1002/jgrd.50528

Dupont S., *et al*., 2021. Comparison between Eddy-Covariance and flux-gradient size-resolved dust fluxes during wind erosion events. *J. Geophys. Res. Atmos*., 126 (13), e2021JD034735. https://doi.org/10.1029/2021JD034735

Foken T., *et al*., 2012. The Eddy Covariance method. *In*: Aubinet M., *et al*., eds, *Eddy Covariance*, Springer, Dordrecth, 1-19. https://doi.org/10.1007/978-94-007-2351-1_1

Fotiadi A.K., *et al*., 2005. Methodological development of the conditional sampling method. Part I: Sensitivity to statistical and technical characteristics. *Bound. Lay. Meteorol*., 114 (3), 615-640. https://doi.org/10.1007/s10546-004-1080-9

Francis D., *et al*., 2022. Atmospheric rivers drive exceptional Saharan dust transport towards Europe. *Atmos. Res.*, 266, 105959. https://doi.org/10.1016/j.atmosres.2021.105959

Fratini G., *et al*., 2007. Size-segregated fluxes of mineral dust from a desert area of northern China by eddy covariance. *Atmos. Chem. Phys*., 7 (11), 2839-2854. https://doi.org/10.5194/acp-7-2839-2007

Gillette D.A., Passi R., 1988. Modeling dust emission caused by wind erosion. *J. Geophys. Res. Atmos.*, 93 (D11), 14233-14242. https://doi.org/10.1029/JD093iD11p14233

Hersbach H., *et al*., 2020. The ERA5 global reanalysis. *Q. J. Roy. Meteor. Soc*., 146 (730), 1999-2049. https://doi.org/10.1002/qj.3803

Huffman J.A., *et al*., 2020. Real-time sensing of bioaerosols: Review and current perspectives. *Aerosol Sci. Tech.*, 54 (5), 465-495. https://doi.org/10.1080/02786826.2019.1664724

Jimenez D.A., *et al*., 2024. Assessing downscaling techniques for frequency analysis, total precipitation and rainy day estimation in CMIP6 simulations over hydrological years. *Hydrol. Earth Syst. Sci.*, 28 (9), 1981-1997. https://doi.org/10.5194/hess-28-1981-2024

Kaimal J.C., *et al*., 1976. Turbulence structure in the convective boundary layer. *J. Atmos. Sci.*, 33 (11), 2152-2169. https://doi.org/10.1175/1520-0469(1976)033<2152:TSITCB>2.0.CO;2

Katul G.G., *et al*., 2014. Two phenomenological constants explain similarity laws in stably stratified turbulence. *Phys. Rev. E*, 89 (2), 23007. https://doi.org/10.1103/PhysRevE.89.023007

Leelőssy Á., *et al*., 2014. Dispersion modeling of air pollutants in the atmosphere: A review. *Cent. Eur. J. Geosci*., 6 (3), 257-278, https://doi.org/10.2478/s13533-012-0188-6

Lighthart B., Shaffer B.T., 1994. Bacterial flux from chaparral into the atmosphere in mid-summer at a high desert location. *Atmos. Environ*., 28 (7), 1267-1274. https://doi.org/10.1016/1352-2310(94)90273-9

Lin H., *et al*., 2023. Deep learning downscaled high-resolution daily near surface meteorological datasets over East Asia. *Sci. Data*, 10 (1), 890. https://doi.org/10.1038/s41597-023-02805-9

Lindemann J., Upper C.D., 1985. Aerial dispersal of epiphytic bacteria over bean-plants. *Appl. Environ. Microb*., 50 (5), 1229-1232.

Lindemann J., *et al*., 1982. Plants as sources of airborne bacteria, including ice nucleation-active bacteria. *Appl. Environ. Microb*., 44 (5), 1059-1063.

Mayol E., *et al*., 2014. Resolving the abundance and air-sea fluxes of airborne microorganisms in the North Atlantic Ocean. *Front. Microbiol.*, 5, 557. https://doi.org/10.3389/fmicb.2014.00557

Monin A.S., Obukhov A.M., 1954. Basic laws of turbulent mixing in the surface layer of the atmosphere. *Contrib. Geophys. Inst. Acad. Sci. USSR*, 24 (151), 163-187.

Moore R.A., *et al*., 2021. Climatic and landscape changes as drivers of environmental feedback that influence rainfall frequency in the United States. *Glob. Change Biol*., 27, 6381-6393. https://doi.org/10.1111/gcb.15876

Mora C., *et al*., 2022. Over half of known human pathogenic diseases can be aggravated by climate change. *Nat. Clim. Change*, 12 (9), 869-875. https://doi.org/10.1038/s41558-022-01426-1

Morris C.E., *et al*., 2014. Bioprecipitation: A feedback cycle linking Earth history, ecosystem dynamics and land use through biological ice nucleators in the atmosphere. *Glob. Change Biol*., 20 (2), 341-351. https://doi.org/10.1111/gcb.12447

Myneni R.B., *et al*., 1995. The interpretation of spectral vegetation indexes. *IEEE Trans. Geosci. Remote Sens.*, 33 (2), 481-486. https://doi.org/10.1109/TGRS.1995.8746029

NOAA (National Geophysical Data Center), 2009. ETOPO1 1 Arc-Minute Global Relief Model. NOAA National Centers for Environmental Information. Accessed 10/01/2025.

Raupach M.R., Lu H., 2004. Representation of land-surface processes in aeolian transport models. *Environmental Modelling & Software*, 19 (2), 93-112. https://doi.org/10.1016/S1364-8152(03)00113-0

Rinne H.J.I., *et al*., 2001. Disjunct eddy covariance technique for trace gas flux measurements. *Geophys. Res. Lett.*, 28 (16), 3139-3142. https://doi.org/10.1029/2001GL012900

Stiperski I., Calaf M., 2023. Generalizing Monin-Obukhov Similarity Theory (1954) for complex atmospheric turbulence. *Phys. Rev. Lett*., 130 (12), 124001. https://doi.org/10.1103/PhysRevLett.130.124001

Stull R.B., 1988. Mean boundary layer characteristics. *In*: Stull R.B., ed., *An Introduction to Boundary Layer Meteorology*, Springer Netherlands, 1-27. https://doi.org/10.1007/978-94-009-3027-8_1

Turnipseed A.A., *et al*., 2009. The use of disjunct eddy sampling methods for the determination of ecosystem level fluxes of trace gases. *Atmos. Chem. Phys*., 9 (3), 981-994. https://doi.org/10.5194/acp-9-981-2009

Waggoner P., 1973. The removal of *Helminthosporium maydis* spores by wind. *Phytopathology*, 63 (10), 1252. https://doi.org/10.1094/Phyto-63-1252

Webb E.K., *et al*., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Q. J. R. Meteorol. Soc*., 106, 85-100. https://doi.org/10.1002/qj.49710644707

Wéry N., *et al*., 2017. Bioaerosol Sources. *In*: Delort A.-M., Amato P., eds., *Microbiology of Aerosols*, Wyley, 115-135. https://doi.org/10.1002/9781119132318.ch2a

Chapter 4

Modelling the transport of microorganisms: What can we learn from particle transport models?

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Solid or liquid particles with diameter typically smaller than 10 μm are present in the atmosphere, where they can have an impact on human health, cloud formation, visibility, crop productivity, output of photovoltaic plants, etc. Therefore, there has been a long-standing interest in being able to understand and represent the life cycle of these particles, also known as aerosols.

Originally, the efforts for modelling atmospheric aerosol stemmed primarily from the concern for human health, and the necessity to anticipate and predict atmospheric pollution episodes. The total amount of particulate matter with aerodynamic diameter D<10 μm (PM_{10}) and with D<2.5 μm ($PM_{2.5}$) are targeted by air quality policies and guidelines issued by governments and by the World Health Organization to monitor and limit air pollution. Along with *in situ* measurements, numerical modelling of aerosols is a tool to forecast and assess compliance of these regulatory norms. Since then, intensive interest has also been taken in the climate impacts of aerosols through their interaction with radiation and clouds, which contributed substantially to the progress in aerosol modelling.

Historically, the attention of atmospheric modellers has been focused on the regulated PM_{10} aerosols. These particles include a variety of species such as black carbon and organic carbon particles from combustion processes, secondary inorganic aerosols such as sulphates, nitrates and ammonium, sea-salt particles, mineral dust, secondary organic aerosols due to the condensation of oxidized volatile organic compounds, and others. Larger particles of interest in the atmosphere include the so-called giant particles of mineral dust and volcanic ash, which can be emitted in large quantities and very high into the atmosphere. Such big particles tend to have a short atmospheric lifetime because they settle rapidly towards the ground. More recently, biological aerosols with an allergenic potential such as pollen or spores have emerged as a topic of interest in the atmospheric modelling community.

The ability to model the nature and amount of atmospheric aerosols depends on the knowledge of their emissions (including both natural and anthropogenic sources) as illustrated in Chapter 3, the representation of the complex physico-chemical processes

that lead to the nucleation of fresh aerosol particles in the atmosphere, the understanding of the microphysics of aerosol-cloud interactions, and the modelling of their transport and removal in the atmosphere through deposition processes. The focus of this chapter is the modelling of the transport of particles in the atmosphere, their settling and deposition, and the quantification of their long-range transport in the atmosphere. Finally, an outlook into how the current state of transport modelling can be applied to biological particles is presented in the last part. In this chapter, the reader will encounter terms and some equations that were also presented in Chapter 3 about emissions and flux.

⏩ Lagrangian vs. Eulerian modelling for atmospheric advection

Tracers in motion in the atmosphere are carried by dry air. The density and mass flux of air obey the continuity equation (Equation 4.1):

$$\frac{\partial \rho}{\partial t} + \nabla \cdot (\rho u) = 0$$

where u is the (3-dimensional) wind speed and ρ is the density of air. This equation reflects mathematically the fact that the total mass of air needs to be conserved: the time derivative of density is equal and opposite to the divergence of the mass flux.

Let us suppose that an inert tracer X is advected by dry air. The mass of this tracer obeys a similar equation (Equation 4.2):

$$\frac{\partial \rho_X}{\partial t} + \nabla \cdot (\rho_X u) = 0$$

where ρ_X is the concentration of X (mass of X per unit volume). For atmospheric advection, it can be interesting to advect the mixing ratio of X (Equation 4.3):

$$a_X = \frac{\rho_X}{\rho}$$

rather than its concentration, because tracer mixing ratio is conserved along trajectories (while tracer concentration is not, due to the compressibility of air; Equation 4.4): α

$$\frac{da_X}{dt} = 0$$

or equivalently (Equation 4.5):

$$\frac{\partial a_X}{\partial t} + u \cdot \nabla a_X = 0$$

In particular, if α_X is uniform initially (a well-mixed tracer), then it must stay uniform throughout the experiment. Numerical resolution of Equation 4.2 ("flux form") guarantees conservation of tracer mass, while numerical resolution of Equation 4.5 guarantees the conservation of uniform mixing ratios. Both properties are desirable but are difficult to obtain simultaneously in chemistry-transport models because (generally) the continuity Equation 4.1 is not strictly verified for several reasons such as interpolation in space and time, or data assimilation (see e.g. Jöckel *et al.*, 2001; Lachatre *et al.*, 2020).

There are two approaches to solve this equation for atmospheric transport modelling purposes, called the Lagrangian and the Eulerian approach (Brasseur and Jacob, 2017;

Leelossy *et al.*, 2016). Generally speaking, Lagrangian approaches are very appropriate to simulate sharp, isolated plumes, but Eulerian models combine better with the resolution of nonlinear atmospheric chemistry. Therefore, the Eulerian approach is much more widespread in general-purpose chemistry-transport models, while the use of Lagrangian models is popular when it comes to dealing with isolated plumes with little to no chemistry (volcanic ash plumes, radioactive plume...).

The Lagrangian approach

The Lagrangian approach consists in solving Equation 4.4 by following air parcels along their trajectory and using the fact that air parcels do not mix with each other under pure advection (Brunner, 2012): the mixing ratio of inert tracers in a particular air parcel during its atmospheric travel stays constant, as reflected by Equation 4.4. Evidently, pure advection is not really occurring in the atmosphere. In particular, there is always some degree of mixing (strong in the planetary boundary layer, weaker in the free troposphere, and extremely weak in the stratosphere). Mixing in Lagrangian models is usually considered in the vertical direction only and taken into account by adding a random vertical motion to air parcels, proportional to the expected intensity of vertical mixing. Removal from the atmosphere by dry and wet deposition processes can also be accounted for (Bakels *et al.*, 2024; Van Leuven *et al.*, 2023).

Lagrangian models are very useful to simulate isolated plumes of inert or weakly reactive tracers such as radioactive isotopes (Hanfland *et al.*, 2024; Long *et al.*, 2019; Nabavi *et al.*, 2023) or volcanic ash (Dacre *et al.*, 2016; Plu *et al.*, 2021). This is due to the fact that, by design, Lagrangian models are able to reduce or suppress undesirable numerical diffusion. The Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) model (Stein *et al.*, 2015) and the FLEXible PARTicle (FLEXPART) dispersal model (Bakels *et al.*, 2024; Pisso *et al.*, 2019) are among the most largely used transport models in this category. Lagrangian models are not only used for trajectory studies: they can provide three-dimensional outputs and include active chemistry, even though tropospheric chemistry is often limited to linear chemistry only (Bakels *et al.*, 2024; Henne *et al.*, 2012). As a matter of fact, Lagrangian chemistry-transport models are not common, and most chemistry-transport models are designed with a Eulerian approach (Brunner, 2012; Henne *et al.*, 2012). In the stratosphere, where the role of turbulence and mixing is less prevalent, Lagrangian chemistry-transport models have been developed and used with success, such as ATLAS (Alfred Wegener InsTitute LA grangian Chemistry/Transport System; Wohltmann *et al.*, 2010) and the Chemical Lagrangian Model of the Stratosphere (CLaMS) (Charlesworth *et al.*, 2020).

The Eulerian approach

The Eulerian approach consists in solving Equation 4.5 using a gridded representation, dividing the atmosphere (or a regional portion of the atmosphere) into fixed elementary volumes, treating tracer concentration in each of these volumes as a prognostic variable. Various techniques can be implemented for the resolution of these equations. Popular methods for atmospheric advection include the use of the Piecewise Parabolic Method introduced by Colella and Woodward (1984), or of variants thereof. Using Eulerian models rather than Lagrangian models have both advantages and drawbacks. The key advantage of Eulerian modelling is that it directly provides a regular solution for the

entire domain, permitting the inclusion of nonlinear physical and chemical processes in a direct way, which is very important for chemistry-transport model. Therefore, models of atmospheric pollution including atmospheric chemistry are often designed with a Eulerian strategy (Brasseur and Jacob, 2017). One classical drawback of Eulerian resolution of the advection is that it tends to introduce excess numerical diffusion compared to Lagrangian models (Brasseur and Jacob, 2017). As a result, Lagrangian models tend to perform better in representing the fine-scale, filamentary structures that tend to appear in atmospheric flows (Khosrawi *et al.*, 2005). In spite of this intrinsic limitation, Eulerian models have been used successfully even for the advection of sharp localized plumes such as volcanic or radioactive plumes, with models such as Fall3d, Ash3d or CHIMERE (Adenis *et al.*, 2024; Folch *et al.*, 2020; Prata *et al.*, 2021; Schwaiger *et al.*, 2012).

⏩ Specificity of particle transport

Particles do not behave like gas tracers for a variety of reasons:
– They do not exactly follow the flow of the carrying fluid (air) because they have a settling speed due to the effect of gravity;
– They can collide with the ground or vegetation, and be intercepted by hydrometeors;
– They can act as cloud condensation nuclei or ice nucleating particles, *i.e.* influence the formation and properties of clouds.

Emissions of natural aerosols

One indispensable prerequisite for modeling aerosol transport is information on emission fluxes into the atmosphere. Although the topic of bioaerosol emissions is covered in Chapters 3, 7 and 8, the main mechanisms of emission of common primary natural aerosols, as described in models, are briefly introduced here.

Dust emissions

Under the action of wind, erodible layers of soil can release particles of mineral dust into the atmosphere. Typically, mineral dust emissions activate when surface wind speed reaches a threshold friction velocity, which depends on the surface type, its roughness, and the size of the emitted particle. The flux then usually increases as a power law of friction velocity (Alfaro and Gomes, 2001; Kok *et al.*, 2014; Marticorena and Bergametti, 1995).

Sea spray emissions

Similar to dust, sea salt and organic matter at the surface of the ocean can be lifted up into the atmosphere under the action of wind. The emission flux is commonly represented as a power law of wind speed and a scaling parameter related to the size of the emitted particles (Gong *et al.*, 1997). Second order parameters that also affect the sea spray flux and are sometimes introduced in parameterizations are sea surface temperature and sea water salinity (Mårtensson *et al.*, 2003).

Settling of atmospheric aerosol: Influence of particle characteristics

Condensed particles in the atmosphere do not follow exactly the atmospheric flow because they are denser than the surrounding air (see e.g. Du *et al.* (2023) for a

description of the density of various types of organic and inorganic aerosols). The simplest way to describe the settling speed of aerosol particles is to use the Stokes (1851) formula describing the drag force applied by air on the particle. This yields the following expression for the settling speed of a spherical particle with diameter D (Equation 4.6):

$$v_\infty = \frac{gD^2\left(\rho_p - \rho_a\right)}{18\mu}$$

where ρ_p is the density of the particle, ρ_a the density of air, g the acceleration of gravity and μ the dynamic viscosity of air, which is a function of temperature only and can be calculated using the formulation given in NOAA/NASA/USAF (1976). Equation 4.6 is valid exactly provided that (i) the particle is much larger than the mean-free path of air molecules, and (ii) the Reynolds number (Re) of the flow is extremely small. Empirical formulations for the deviations to this law exist. The most used in atmospheric sciences are the Davies (1945) slip-correction factor (for small particles), and the Clift and Gauvin (1971) drag reduction for large particles with non-negligible Reynolds number. Details and explicit formula for the deviations of the settling speed from the Stokes law for both small and big particles are given in Mailler *et al.* (2023). As a consequence of the D^2 dependency in Equation 4.6, in part mitigated by the drag reduction for large particles (substantial for Re>0.1), the settling speed of particles increases very strongly as a function of their diameter: A particle with D≈10 μm settles with vertical speed 10^{-2} m/s (almost 1,000 m in a day, which is substantial). On the other hand, a particle with diameter D≈1 μm settles 100 times slower, about 10^{-4} m/s (less than 10 m in a day). Therefore, for micron or sub-micron particles, gravitational settling is practically negligible.

Conversely, for "giant" particles with D>10 μm, settling speed increases very strongly, which suggests a very short atmospheric lifetime for such particles. In theory, the deposition velocity of particles with D>100 μm should reach or exceed 1 m/s (Figure 4.1a). In other words, they should settle almost immediately and not be transported far from their source. And yet, giant dust particles with diameter up to 450 μm have been collected in the atmosphere over the Atlantic Ocean, thousands of kilometers away from the nearest emerged land (van der Does *et al.*, 2018).

Non-sphericity of such giant particles could explain a part of their unexpectedly strong ability to remain airborne over thousands of kilometers, as suggested by the effect of non-sphericity on aerodynamic propertied described in Chapter 2. The assumption of sphericity is justified for liquid particles –with the notable exception of falling raindrops– because surface tension is sufficiently strong to maintain sphericity of liquid particles in the atmosphere. However, this assumption is not justified for solid particles, which can have a variety of shapes that deviate strongly from sphericity (see Okada *et al.* (2001) and Yang *et al.* (2013) for mineral dust, and Liu *et al.* (2015) and Riley *et al.* (2003) for volcanic ash). Shape and size diversity is also extremely strong for microplastic fragments or fibers, an emerging topic of concern (Goral *et al.*, 2023). Shape influences the settling speed of particles, with irregular-shaped particles typically falling slower than a spherical particle of the same volume (Yang *et al.*, 2013). Classical empirical formulations for the settling speed of irregular-shape particles include Ganser (1993) and Wilson and Huang (1979). The fact that irregular particles fall slower than same-volume spheres is due to their dynamical tendency to fall exposing their

largest section across the flow (Bhowmick *et al.*, 2024; Mallios *et al.*, 2021), and that with this orientation the drag is stronger than for the same-volume spherical particle (Mailler *et al.*, 2024; Mallios *et al.*, 2020). For prolate spheroids for example, settling speed is reduced by ≈10% when the aspect-ratio is equal to 2, and ≈20% when it reaches 4 (Figure 4.1b). The relatively modest magnitude of this effect suggests that non-sphericity can contribute to the longer-than-predicted atmospheric lifetime of certain giant atmospheric particles, but that it is not sufficient fully explain this.

As a consequence, modellers who try to represent long-range transport of giant dust particles still need to include empirical reduction factors to the settling speed of the biggest particles. Apart from the effect of non-sphericity, these empirical reduction factors can be seen as a combined representation of several processes such as vertical mixing in the dust layers, unresolved turbulence or other meteorological conditions, and electrical effects (Drakaki *et al.*, 2022).

For the purpose of modelling the atmospheric transport of bioaerosols, knowledge of their size and shape is therefore an important prerequisite to accurately represent their settling speed, lifetime and distances they can travel in the atmosphere.

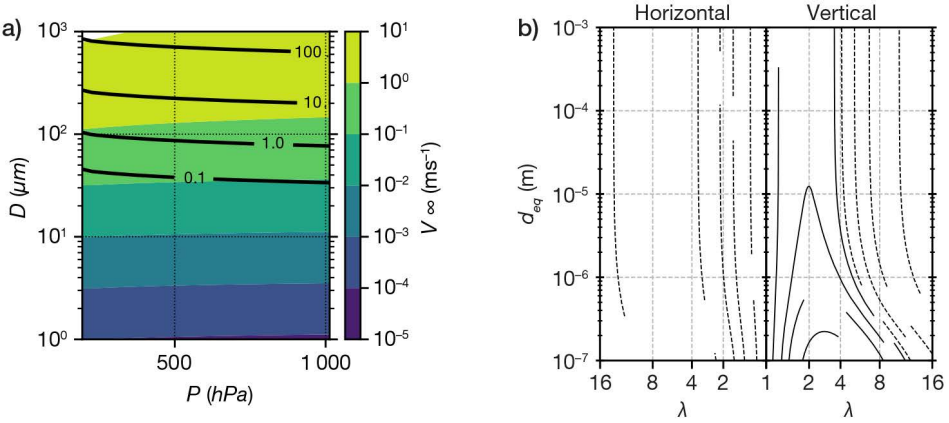

Figure 4.1. Particle settling speeds.

a. Settling speed of a spherical particle in m/s as a function of particle diameter and atmospheric pressure (color shading), and Reynolds number of the particle (contours). The density of the particle is ρ=2650 kg/m^3, and temperature is estimated from pressure based on the US Standard atmospheric profile (NOAA/NASA/USAF, 1976). Black lines represent the Reynolds number of the flow (Re). For Re>0.1, it is necessary to take into account large-particle drag correction. Figure adapted from Mailler *et al.*,(2023). **b.** Difference of the settling speed of a prolate spheroidal particle with ρ=2650 kg/m^3 compared to the same-volume sphere. d_{eq} is the mass-equivalent diameter of the particle, and λ its aspect ratio. Left and right panel of the plot give the relative speed difference depending on horizontal and vertical orientation, respectively. Figures adapted from Mailler *et al.* (2024). The fate of atmospheric aerosol: dry and wet deposition.

Aerosols can be removed from the atmosphere through two processes: Wet deposition *i.e.* scavenging by clouds and precipitation, and dry deposition *i.e.* turbulent processes and gravitational settling which bring particles back to the surface. The representation of deposition in models strongly conditions the aerosol atmospheric budget. This section describes briefly and generally the approach of chemistry-transport models to represent aerosol dry and wet deposition.

Dry deposition

In atmospheric models, the dry deposition velocity of aerosols (V_d) (referred to as terminal velocity in Chapter 2) is typically represented as the combination of a gravitational settling term (V_g) and of a resistance term corresponding to aerodynamic (R_a) and surface (R_s) resistances. As an illustration, the dry deposition formulation from Zhang *et al.* (2001) is provided and detailed hereafter. The gravitational settling term is given by Equation 4.7:

$$V_g = \frac{\rho_p d_p^2 g C}{18\mu}$$

with ρ_p the density of the particle, d_p the particle diameter, g the gravitational acceleration, C a correction factor for small particles and μ the dynamic viscosity of air.

The aerodynamic resistance (Equation 4.8) is:

$$R_a = \frac{\log\left(\frac{z_R}{z_0}\right) - \Psi_H}{ku*}$$

with z_R the height at which the dry deposition velocity V_d is evaluated, z_0 the surface roughness length, Ψ_H a stability function, κ the Von Karman constant, $u\star$ the friction velocity. The individual terms are not detailed here but the interested reader is invited to consult Zhang *et al.* (2001).

The surface resistance (Equation 4.9) is:

$$R_s = \frac{1}{\varepsilon_0 u*\left(E_B + E_{IM} + E_{IN}\right) R}$$

with ε_0 an empirical coefficient, R a correction factor for the fraction of particles that stick to the surface, and E_B, E_{IM} and E_{IN} the collection efficiency from Brownian diffusion, impaction and interception, respectively.

Finally, based on the previous formula, the deposition velocity (Equation 4.10) follows:

$$V_d = V_g + \frac{1}{R_a + R_s}$$

In this formulation, the particle-dependent parameters governing deposition velocity are its diameter and density (through the gravitational settling term). The other terms describing deposition depend on meteorology (wind speed, air density...) or surface properties (vegetation type, water surface...). Therefore, such an approach for dry deposition modelling can be readily transferred to biological particles, provided their sizes and densities are known (see Chapter 2). For example, the formulation for aerosol dry deposition was applied to the modelling of bacteria in the EMAC model (Burrows *et al.*, 2009), with bacteria represented as aerosols of typical size around 1 μm and 1 g/cm^3 density.

Although the formulation presented here is typical of how dry deposition is represented in models, several variants exist with different fit coefficients and parameter values depending on the measurements they are based upon. This results in a large

uncertainty in deposition velocity, with up to more than one order of magnitude difference in velocity for a 1 μm particle across the commonly used parameterizations (Saylor *et al.*, 2019), which in turn can lead to major uncertainties in surface concentrations.

Wet deposition

Wet deposition typically comprises two terms, one representing the scavenging occurring inside clouds, and one for the washout of particles below precipitating clouds.

Below-cloud scavenging occurs when precipitation impacts aerosols present in the atmosphere below clouds and brings them to the ground in the process. Scavenging by rainfall or snow is usually represented separately, as droplets and snowflakes remove aerosols differently. For liquid clouds, scavenging is parameterized based on cloud droplet sizes, precipitation rate and aerosol diameters (e.g., Willis and Tattelman, 1989). Although parameterized with different equations, below-cloud scavenging by snow also essentially depends on the aerosol size (e.g., Wang *et al.*, 2014). Similar to dry deposition, below-cloud scavenging generally depends on the aerosol size and density. Therefore, below-cloud scavenging of bioaerosols in models can readily use existing parameterizations.

In-cloud scavenging can occur through the activation of aerosols to form droplets (cloud condensation nuclei, CCN) or ice crystals (ice nucleating particles, INP), or through the impaction of aerosols by existing cloud droplets. When aerosols are impacted, they are integrated into the droplet and can either be re-mobilized in the atmosphere if the droplet evaporates, or precipitate if rainfall occurs. The activation of aerosols into droplets is best described by the Köhler (1936) theory, although the associated equations cannot be solved directly. Instead, models rely on parameterizations based on measurements which associate water vapor supersaturation levels and number concentration of aerosols that can act as CCN to derive how many droplets are formed and their associated size. The effect of aerosols on cloud microphysics can then be represented based on the number and mass of aerosols in the atmosphere that have the ability to act as CCN (e.g., Morrison *et al.*, 2005).

Bioaerosols as CCN and INP

Biological particles such as spores, pollen, or bacteria, have been shown to have the ability to act as CCN (Möhler *et al.*, 2007; Pope, 2010), but the Köhler theory seems to not account well for the hygroscopic behavior of organic material (Sun and Ariya, 2006). Therefore, more investigative effort is required to better understand and represent the role of bioaerosols as CCN. Under colder temperatures (at high altitude/latitude), biological particles are also an important source of INP (Chatziparaschos *et al.*, 2024; Pereira Freitas *et al.*, 2023). In particular, they are relevant for relatively warmer INPs, as opposed to dust aerosols which are the dominant species responsible for ice nucleation at very low temperature. The representation of ice nucleation processes in models is still challenging, both from the identification of the aerosol species capable of acting as INP and because of a lack of understanding of some of the underlying physical processes (Burrows *et al.*, 2022).

Importantly, the interactions between aerosols and cloud microphysics are currently one the most uncertain processes in models. Including a representation

of bioaerosols acting as CCN and INP could help better constrain the Earth's radiative budget, especially in the context of a changing climate (Creamean *et al.*, 2013; Ontiveros *et al.*, 2021). More details about biological INP are provided in the Introduction and in Chapters 3, 7 and 8.

⏩ Quantifying the long-range transport of particles

Aerosols can travel through the atmosphere over thousands of kilometers (see Chapter 1), depending on their properties such as shape, size, density and hygroscopicity, which determine their lifetime. Quantifying such a transport (e.g., determine how much mass or how many particles reach a certain location) in a systematic manner is not straightforward. For this, modelling is an adequate tool as it represents concentrations of particles continuously through time and space. Furthermore, the possibility to simulate scenarios and conduct sensitivity studies can provide insightful results on the transport of particles.

Hereafter are provided some examples of model-based approaches which successfully provide quantitative estimates of the transport of aerosols. The most commonly used methods rely on Eulerian models, which provide temporal and spatial distributions of concentrations and mass fluxes of aerosols. Lagrangian models can also be used to identify sources regions of particles. The three main methods are summarized in Figure 4.2.

Tagging emissions

One approach to quantifying the transport of aerosols depending on their geographical origin (continent, city, specific location) consists in tagging emissions in simulations using a Eulerian chemistry-transport model (as represented schematically in Figure 4.2a). Typically, the method used in Liu *et al.* (2009) is such an example. In their work, they use a global coupled chemistry-aerosol model and tag emissions of primary aerosol for each continent, with a different name (but identical properties). With such an approach they can compare the effect on atmospheric composition of domestic emissions versus long-range transport from other continents, by comparing the concentrations of the different tagged species at a given location or over a given area. For example, Liu *et al.* (2009) found that background mineral dust over most continents contains a large contribution from African dust sources.

Emission tagging can be used at different scales and applied to emission sectors (e.g., traffic, residential, industry...) in addition to/instead of geographical locations, to evaluate the burden on air quality of emissions from a given pollution source or emissions of a large city on the neighboring areas (e.g., Lapere *et al.*, 2021a, 2021b). Interestingly, for small arthropods that are transported by wind, capture and release experiments –similar to emission tagging– are part of the demographic toolbox to trace their dispersal pathways as described in Chapter 11.

Fluxes into receptor regions

Reanalysis datasets such as CAMS (Inness *et al.*, 2019) or MERRA-2 (Gelaro *et al.*, 2017) provide global model realizations over long time scales (decades) and at intermediate resolution (around 0.5°), which incorporate observed data to drive the

chemistry-transport model through assimilation. Although tagging of particles like in the previous example is not possible for the end-user, quantification of aerosol transport can still be done, especially to quantify how much aerosol mass is transported into/outside a region of interest.

For example, Böö *et al.* (2023) quantified the amount of mineral dust particles transported into the Arctic from the lower latitudes using CAMS and MERRA-2. To do so, they defined a receptor region with boundary latitudes and longitudes and computed the vertically integrated fluxes of aerosols through the boundary of this region. For this particular case, the vertically integrated flux (Equation 4.11) is defined as:

$$\Phi(x) = \int_0^{TOA} Vx \; dp$$

with V the zonal and meridional wind speed and x the mixing ratio of interest (water vapor, aerosol...), at pressure level p. For this case, Φ uses only the meridional transport component as the receptor region is the Arctic. However, the method can be applied to any region, provided the wind components used to project the transport are chosen accordingly (see Figure 4.2b).

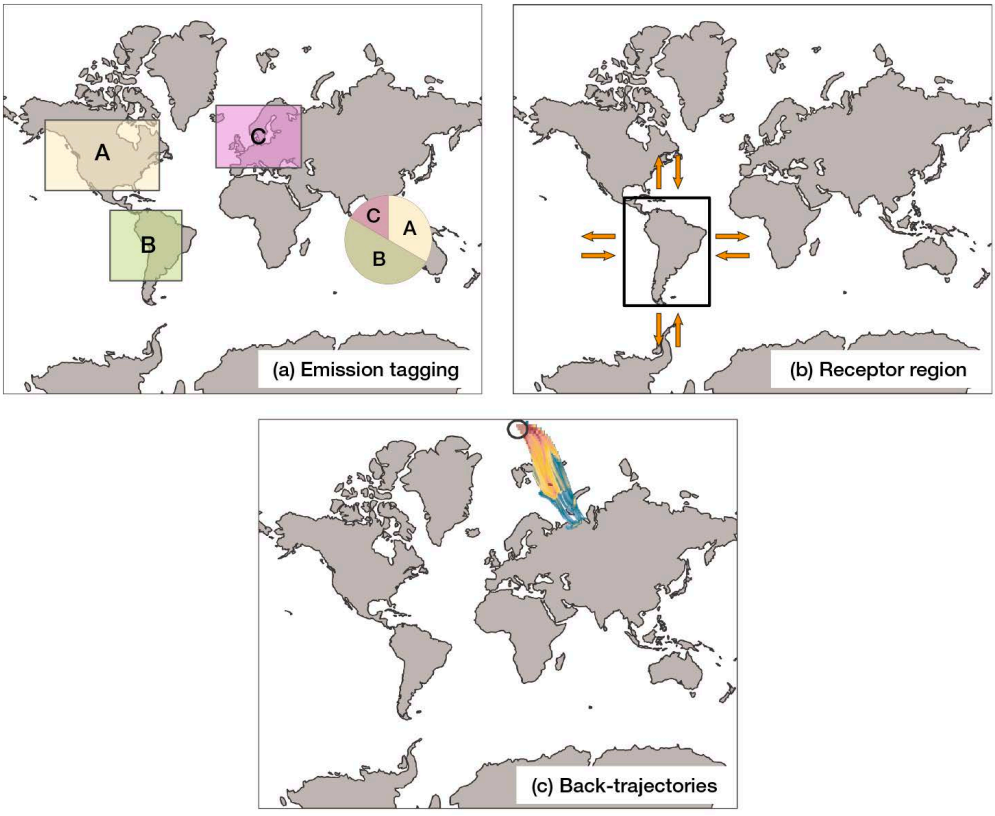

Figure 4.2. Examples of methods for quantifying aerosol transport.

(**a**) Tagging of emissions in model experiments. (**b**) Quantification of aerosol fluxes into a receptor region. (**c**) Residence time of black carbon-containing air masses along a 30-day back-trajectory on 2020-04-15. FLEXPART simulations from the MOSAiC campaign obtained from https://img.univie.ac.at/webdata/mosaic.

Importantly, Böö *et al.* (2023) found major differences in the fluxes obtained using CAMS versus MERRA-2, highlighting the large uncertainty still associated with reanalysis products. Despite applying the same methodology for both datasets and similar global emission fluxes in both, the result in dust transported into the Arctic was different by more than one order of magnitude. This exemplifies how representing the life cycle of aerosols (transport, deposition) is still a challenge in atmospheric chemistry models.

This method for quantifying aerosol fluxes can also be applied to extreme cases, which are then referred to as aerosol atmospheric rivers (AAR). They are defined in an analogous way as atmospheric rivers (AR), which are extreme events of horizontal transport of water vapor (Nash *et al.*, 2018; Shields *et al.*, 2018; Wille *et al.*, 2019; Zhu and Newell, 1998) but looking at the horizontal flux of aerosols instead of water vapor. Definitions and classification criteria, as well as climatologies of AAR events, can be found in Chakraborty *et al.* (2021, 2022) and Lapere *et al.* (2024).

Typically, the vertically integrated flux of quantity x (x the aerosol mixing ratio) is computed as in Equation 4.11 (up to a factor applied for dimensionality that is not introduced here for simplicity of reading) over the meridional and zonal directions, based on model or reanalysis data. Then, at each time step, if the flux in a grid cell is above a pre-determined threshold, the grid cell is counted as an AAR-participating point. When an area of continuous AAR-participating points is elongated enough (with respect to some threshold aspect ratio and minimum length), an AAR is detected and counted. Note that for poleward transport of aerosols, usually only the meridional component is considered, and the threshold definition and shape criteria change compared to mid-latitude AAR (Lapere *et al.*, 2024).

Such algorithms provide an approach for the systematic detection of aerosol transport events. However, because this method is based on modelling, it depends on the ability of the model to correctly represent horizontal advection and is limited to variables included in the model.

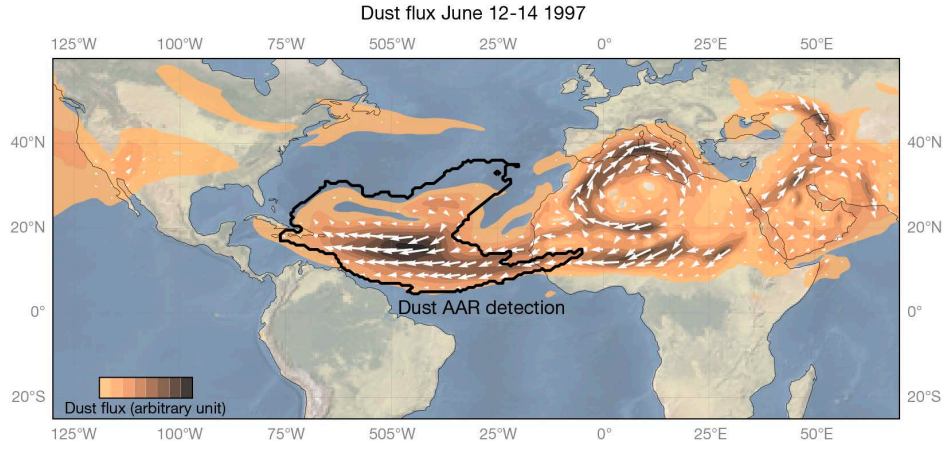

Figure 4.3. Example of dust episode detected as an aerosol atmospheric river.

Total dust flux (colormap and arrows) and dust aerosol atmospheric river detection (contour) on June 12-14 1997. Dust fluxes are from MERRA-2 and dust AAR detection is from the Chakraborty *et al.* (2022) AAR catalog. This date corresponds to the case study of inter-hemispheric bacteria and fungi transport associated with dust from Prospero *et al.* (2005).

Although AAR detection is currently applied to common aerosols such as black carbon, dust or sea salt, the underlying principle could also be applied to any type of aerosol, including biological particles, pollen, spores, microbes, etc. Although such species are yet to be included in atmospheric models, AAR can still provide valuable information. Long-range transport of biological particles such as fungi or bacteria typically occurs in correlation with the transport of natural aerosols such as dust or sea spray (Prospero *et al.*, 2005; Reche *et al.*, 2018). Therefore, analyzing the extreme events of aerosol transport detected as AAR in a systematic manner could provide information regarding the transport pathways and transported quantities of microorganisms. This is illustrated in Figure 4.3, which shows the case study from Prospero *et al.* (2005) who found increased concentrations of fungi and bacteria in the Caribbean in relation with an event of transatlantic Saharan dust transport.

Back-trajectories

For a given time and place, it is possible to go backwards in time to follow the trajectories of air masses that arrived at this time and place. This approach is referred to as back-trajectories and leverages the use of Lagrangian models such as FLEXPART (Pisso *et al.*, 2019), HYSPLIT (Stein *et al.*, 2015), LAGRANTO (Sprenger and Wernli, 2015)...

This technique is typically applied in the framework of observational case studies where the research question is "where did the measured aerosols originate from?". It uses simulated meteorological fields (from models, global or regional and/or reanalysis) to trace back the most likely origin of air masses, at different vertical levels in the atmosphere, including their residence time over areas along the trajectories. This is illustrated in Figure 4.2c, with an example from the Arctic expedition MOSAiC (Shupe *et al.*, 2022) when an intrusion of aerosols within a warm air mass was recorded (Dada *et al.*, 2022). In this case, the FLEXPART model, computing back-trajectories based on the ERA5 meteorological reanalysis, showed that the spike in aerosols recorded near the North Pole was most likely due to long-range transport coming from Eurasia.

However, the results from analyses based on back-trajectory methods need to be carefully interpreted. Simple analyses can be unreliable and lead to misinterpretation and misleading source attributions (Da Silva *et al.*, 2024). Chapter 11 presents details about how backwards trajectories have been applied to identifying the dispersal trajectories of biological particles.

⏩ From particles to microorganisms: Challenges for modelling

First bioaerosol modelling attempts

Even though they are usually not included in atmospheric models by default, there have been initiatives to model and quantify the amount and transport of some types of bioaerosols in the global atmosphere.

For example, Burrows *et al.* (2009) included emissions of bacteria in the global atmospheric chemistry model EMAC, represented as aerosol tracers of 1 μm and 3 μm diameter and 1 g/cm^3 density. They found that the atmospheric concentrations and transport of bacteria is primarily sensitive to the assumptions made on the rates of uptake by clouds as CCN or INP. Emission region, particle diameter and seasons were

also factors contributing to variability, although to a lesser extent. This model including bacteria was later used with an inversion of atmospheric transport to reconstruct emission rates of bacteria over different ecosystems, based on available measurements of atmospheric concentrations (Burrows *et al.*, 2013).

Pollen emissions from birch or ragweed have also been implemented in regional chemistry-transport models such as WRF-Chem (Subba *et al.*, 2023; Werner *et al.*, 2021) or CHIMERE (Menut *et al.*, 2021). Good agreement with observations over Europe was obtained, which provided insight into the transport of pollen in the atmosphere, with implications for forecasting exposure and spikes in allergy triggering. The CHIMERE model was also used to study the atmospheric transport of fungal spores in France, with relevance for public health (Vida *et al.*, 2024).

To our knowledge, other types of microorganisms, such as viruses, have yet to be considered in atmospheric chemistry models. However, smaller-scale modeling initiatives following measurement campaigns could be scaled for use in large-scale models. For example, Kobziar *et al.* (2024) used bacterial emission factors measured during a wildfire event to parameterize a computationally scalable particle transport model, which could be interfaced with regional chemistry-transport models. Moore *et al.* (2020) and Kobziar *et al.* (2022) also provide emission factors of bacterial cells and biological INPs measured during prescribed fire events combined with smoke modeling, which could be used as a basis to start considering such species in large-scale atmospheric models. Other small-scale transport modeling, such as for representing virus spread to or among individuals could also be leveraged to inform larger-scale models (Abuhegazy *et al.*, 2020; Dowd *et al.*, 2000).

Aerosolized algae are found in the atmosphere (Sharma *et al.*, 2007) but are yet to be accounted for in atmospheric chemistry models. Algae have both soil and aquatic sources, for which emission into the atmosphere is governed by wind speed, similar to dust and sea spray. Leveraging dust and sea spray emission parameterizations, combined with information on soil/ocean composition could provide a decent first approximation. More generally, primary biological aerosol particles (PBAP) can be emitted from surface waters, in a process similar to sea spray (see Chapter 7). The sea spray process is quite well described in atmospheric models. Hence, relatively small adaptations would be needed to include ocean-sourced PBAP emissions in models (such as those leveraging parameterizations that describe the fraction of organic material in sea-spray) usually based on the concentration of chlorophyll-a in the ocean (Vignati *et al.*, 2010).

Despite the examples above, there is, to our knowledge, no realistic emission inventory of microorganisms, without which models cannot accurately represent their quantities in the atmosphere. Building this inventory should be a priority of the community in this respect as mentioned in Chapter 3.

What we can learn from particle transport modelling

The transport of classical aerosols such as dust, volcanic ash or sea-spray has been modelled for a long time and has reached a relatively mature state in the modelling community. Nevertheless, there are still some challenges as pointed out by model comparison initiatives such as AEROCOM, which show that there can be a large

diversity in the amount of natural aerosols simulated by different models (Gliß *et al.*, 2021). Bioaerosols on the other hand are a more recent topic for atmospheric modelling, although some of the elements needed for including these species in models are readily available. As illustrated by the examples in this chapter, it is possible to obtain a first representation of any biological aerosol in atmospheric models by assuming size and physical properties such as density and the ability of the particle to form clouds. This includes both larger particles that are transported as a single aerosol such as pollen, and smaller particles such as viruses which are usually transported in the atmosphere by being attached to/included in a larger host particle of different origin, such as dust (Després *et al.*, 2012).

For bioaerosols that are not transported individually but onto a classical aerosol, e.g., viruses transported with dust (Olofsson, 1988), knowing the properties of the host aerosol could give a good approximation of the bioaerosol transport. In particular, a first approximation could be to use existing measurements of microorganisms on transported dust or sea spray or in smoke plumes, and apply a factor on the concentrations of these classical aerosols in the model to obtain a first representation of atmospheric concentrations of aerosolized microorganisms.

On the other hand, larger bioaerosols transported individually could also be included in models similar to classical aerosols, provided their size, shape, density and physical properties are known. This first representation can be further refined using inversion techniques based on measurements of atmospheric quantities of the considered microorganism (Burrows *et al.*, 2013). Ultimately, the main limitation for models currently is knowledge of bioaerosol emission processes and fluxes and source regions.

The systematic integration of bioaerosols in models is limited by the availability of observational data, and a better understanding of their physico-chemical properties. Suggested research directions for obtaining a modelling system capable of estimating atmospheric transport and climate and health impacts of bioaerosols include (i) the improvement of analytical techniques for the identification and quantification of bioaerosols, (ii) the development of atmospheric biogeography (*i.e.* understanding the abundance, diversity, seasonal and regional variations of bioaerosols), and (iii) the identification and quantification of emission rates (see Chapter 3), optical properties and cloud formation ability of bioaerosols through field and laboratory experiments (Després *et al.*, 2012).

However, even if these bioaerosol-related barriers are overcome, there are still modelling challenges, even for the transport of classical aerosols, which will therefore also apply to bioaerosols. In particular, as illustrated in this chapter, the shape of particles greatly influences their settling speed, and therefore their lifetime, but this parameter is often ignored in models, which usually assume a spherical shape. Similarly, deposition of aerosols via wet removal in or below clouds represents a large source of uncertainty in models, which will also create uncertainty in the bioaerosol budget, especially for hydrophilic species.

Finally, not only is it of interest for the microorganism research community to have tools modelling the transport of bioaerosols, but it is also of interest for the atmospheric modelling community to include bioaerosols in their models. Indeed, bioaerosols such as PBAP and pollen have been suggested to play an important role in cloud formation (Pope, 2010). Moreover, bioaerosols coated onto another type of aerosol could

alter its physical properties. For example, biological material, mixed with mineral dust particles in the soil or during atmospheric transport, can increase the nucleation ability of dust (Boose *et al.*, 2016). Therefore, modelling bioaerosols, including their interactions with other aerosols, could therefore lead to a better representation of climate in models. Furthermore, as stated in the Introduction of this chapter, one of the original motivations for creating models representing atmospheric composition was for monitoring public health risks stemming from air pollution. Chapter 13 shows that microorganisms transported in the air can also impact human health. Therefore, including such species in atmospheric models can benefit the assessment of and forecast of air pollution-related threats. Overall, the current state of science in the modelling of particle transport and the growing knowledge on bioaerosols represent an opportunity to join efforts and foster interactions between the two communities.

⏩ Literature cited

Abuhegazy M., *et al*., 2020. Numerical investigation of aerosol transport in a classroom with relevance to COVID-19. *Physics of Fluids*, 32 (10), 103311. https://doi.org/10.1063/5.0029118

Adenis L., *et al*., 2024. Lagrangian and Eulerian modelling of 106Ru atmospheric transport in 2017 over northern hemisphere. *J. Environ. Rad.*, 275, 107416. https://doi.org/10.1016/j.jenvrad.2024.107416

Alfaro S.C., Gomes L., 2001. Modeling mineral aerosol production by wind erosion: Emission intensities and aerosol size distributions in source areas. *J. Geophys. Res.: Atmospheres*, 106(D16), 18075-18084. https://doi.org/10.1029/2000JD900339

Bakels L., *et al*., 2024. FLEXPART version 11: Improved accuracy, efficiency, and flexibility. *Geoscientific Model Development*, 17 (21), 7595-7627. https://doi.org/10.5194/GMD-17-7595-2024

Bhowmick T., *et al*., 2024. Inertia induces strong orientation fluctuations of nonspherical atmospheric particles. *Phys. Res. Lett.*, 132 (3). https://doi.org/10.1103/physrevlett.132.034101

Böö S., *et al*., 2023. Transport of mineral dust into the Arctic in two reanalysis datasets of atmospheric composition. *Tellus B*, 75 (1), 13-32. https://doi.org/10.16993/tellusb.1866

Boose Y., *et al*., 2016. Ice nucleating particles in the Saharan Air Layer. *Atmos. Chem. Phys.*, 16 (14), 9067-9087. https://doi.org/10.5194/acp-16-9067-2016

Brasseur G.P., Jacob D.J., 2017. Chap. 7, Numerical methods for advection. *In: Modeling of atmospheric chemistry*, Cambridge University Press.

Brunner D., 2012. Atmospheric Chemistry in Lagrangian Models. Overview. *Geophysical Monograph Series*, 200, 224-234. https://doi.org/10.1029/2012GM001431

Burrows S.M., *et al*., 2009. Bacteria in the global atmosphere – Part 2: Modeling of emissions and transport between different ecosystems. *Atmos. Chem. Phys.*, 9 (23), 9281-9297. https://doi.org/10.5194/acp-9-9281-2009

Burrows S.M., *et al*., 2022. Ice-nucleating particles that impact clouds and climate: Observational and modeling research needs. *Rev. Geophys.*, 60 (2), e2021RG000745. https://doi.org/10.1029/2021RG000745

Burrows S.M., *et al*., 2013. Estimating bacteria emissions from inversion of atmospheric transport: Sensitivity to modelled particle characteristics. *Atmos. Chem. Phys.*, 13 (11), 5473-5488. https://doi.org/10.5194/acp-13-5473-2013

Chakraborty S., *et al*., 2022. Aerosol atmospheric rivers: Climatology, event characteristics, and detection algorithm sensitivities. *Atmos. Chem. Phys.*, 22 (12), 8175-8195. https://doi.org/10.5194/acp-22-8175-2022

Chakraborty S., *et al*., 2021. Extending the atmospheric river concept to aerosols: Climate and air quality impacts. *Geophys. Res. Lett.*, 48 (9), e2020GL091827. https://doi.org/10.1029/2020GL091827

Charlesworth E.J., *et al*., 2020. Impact of Lagrangian transport on lower-stratospheric transport timescales in a climate model. *Atmos. Chem. Phys.*, 20 (23), 15227-15245. https://doi.org/10.5194/ACP-20-15227-2020

Chatziparaschos M., *et al*., 2024. Assessing the global contribution of marine, terrestrial bioaerosols, and desert dust to ice-nucleating particle concentrations. *EGUsphere*, 1-28. https://doi.org/10.5194/egusphere-2024-952

Clift R., Gauvin W.H., 1971. Motion of entrained particles in gas streams. *Can. J. Chem. Eng.*, 49. https://doi.org/10.1002/cjce.5450490403

Colella P., Woodward P.R., 1984. The piecewise parabolic method (PPM) for gas-dynamical simulations. *J. Comput. Phys.*, 11, 38-39. https://doi.org/10.1016/0021-9991(84)90143-8

Creamean J.M., *et al*., 2013. Dust and Biological Aerosols from the Sahara and Asia Influence Precipitation in the Western U.S. *Science*, 339 (6127), 1572-1578. https://doi.org/10.1126/science.1227279

Da Silva A., *et al*., 2024. How to trace the origins of short-lived atmospheric species in the Arctic. *Preprint egusphere*, 2024-2839. https://doi.org/10.5194/EGUSPHERE-2024-2839

Dacre H.F., *et al*., 2016. How accurate are volcanic ash simulations of the 2010 Eyjafjallajökull eruption? *J. Geophys. Res. Atmos.*, 121 (7), 3534-3547. https://doi.org/10.1002/2015jd024265

Dada L., *et al*., 2022. A central arctic extreme aerosol event triggered by a warm air-mass intrusion. *Nat. Comm.*, 13 (1), 1-15. https://doi.org/10.1038/s41467-022-32872-2

Davies C.N., 1945. Definitive equations for the fluid resistance of spheres. *Proc. Phys. Soc.*, 57 (4), 259-270. https://doi.org/10.1088/0959-5309/57/4/301

Després V.R., *et al*., 2012. Primary biological aerosol particles in the atmosphere: A review. *Tellus B: Chemical and Physical Meteorology*, 64 (1), 15598. https://doi.org/10.3402/tellusb.v64i0.15598

Dowd S.E., *et al*., 2000. Bioaerosol transport modeling and risk assessment in relation to biosolid placement. *J. Environ. Qual.*, 29 (1), 343-348. https://doi.org/10.2134/jeq2000.00472425002900010043x

Drakaki E., *et al*., 2022. Modeling coarse and giant desert dust particles. *Atmos. Chem. Phys.*, 22 (18), 12727-12748. https://doi.org/10.5194/acp-22-12727-2022

Du A., *et al*., 2023. Mixing state and effective density of aerosol particles during the Beijing 2022 Olympic Winter Games. *Atmos. Chem. Phys.*, 23 (21), 13597-13611. https://doi.org/10.5194/acp-23-13597-2023

Folch A., *et al*., 2020. FALL3D-8.0: A computational model for atmospheric transport and deposition of particles, aerosols and radionuclides. Part 1: Model physics and numerics. *Geosci. Model Dev.*, 13 (3), 1431-1458. https://doi.org/10.5194/gmd-13-1431-2020

Ganser G.H., 1993. A rational approach to drag prediction of spherical and nonspherical particles. *Powder Tech.*, 77 (2), 143-152. https://doi.org/10.1016/0032-5910(93)80051-B

Gelaro R., *et al*., 2017. The Modern-Era Retrospective Analysis for Research and Applications, Version 2 (MERRA-2). *Journal of Climate*, 30 (14), 5419-5454. https://doi.org/10.1175/JCLI-D-16-0758.1

Gliß J., *et al*., 2021. AeroCom phase III multi-model evaluation of the aerosol life cycle and optical properties using ground- and space-based remote sensing as well as surface in situ observations. *Atmos. Chem. Phys.*, 21 (1), 87-128. https://doi.org/10.5194/ACP-21-87-2021

Gong S.L., *et al*., 1997. Modeling sea-salt aerosols in the atmosphere: 1. Model development. *J. Geophys. Res.: Atmospheres*, 102 (D3), 3805-3818. https://doi.org/10.1029/96JD02953

Goral K.D., *et al*., 2023. Settling velocity of microplastic particles having regular and irregular shapes. *Environ. Res.*, 228, 115783. https://doi.org/10.1016/j.envres.2023.115783

Hanfland R., *et al*., 2024. The Lagrangian Atmospheric Radionuclide Transport Model (ARTM), sensitivity studies and evaluation using airborne measurements of power plant emissions. *Atmos. Chem. Phys.*, 24 (4), 2511-2534. https://doi.org/10.5194/acp-24-2511-2024

Henne S., *et al*., 2012. Global-scale tropospheric lagrangian particle models with linear chemistry. *Geophysical Monograph Series*, 200, 235-250. https://doi.org/10.1029/2012GM001247

Inness A., *et al*., 2019. The CAMS reanalysis of atmospheric composition. *Atmos. Chem. Phys.*, 19 (6), 3515-3556. https://doi.org/10.5194/acp-19-3515-2019

Jöckel P., *et al*., 2001. On a fundamental problem in implementing flux-form advection schemes for tracer transport in 3-dimensional general circulation and chemistry transport models. *Q. J. R. Meteorol. Soc.*, 127 (573), 1035-1052. https://doi.org/10.1002/qj.49712757318

Khosrawi F., *et al.*, 2005. Intercomparison between Lagrangian and Eulerian simulations of the development of mid-latitude streamers as observed by CRISTA. *Atmos. Chem. Phys.*, 585-95. https://doi.org/10.5194/acp-5-85-2005

Kobziar L.N., *et al.*, 2024. Bacterial Emission Factors: A Foundation for the Terrestrial-Atmospheric Modeling of Bacteria Aerosolized by Wildland Fires. *Environ. Sci. Technol.*, 58 (5), 2413-2422. https://doi.org/10.1021/acs.est.3c05142

Kobziar L.N., *et al.*, 2022. Wildland fire smoke alters the composition, diversity, and potential atmospheric function of microbial life in the aerobiome. *ISME Communications*, 2 (1), 8. https://doi.org/10.1038/s43705-022-00089-5

Köhler H., 1936. The nucleus in and the growth of hygroscopic droplets. *Transactions of the Faraday Society*, 32, 1152-1161. https://doi.org/10.1039/TF9363201152

Kok J.F., *et al.*, 2014. An improved dust emission model – Part 1: Model description and comparison against measurements. *Atmos. Chem. Phys.*, 14 (23), 13023-13041. https://doi.org/10.5194/ACP-14-13023-2014

Lachatre M., *et al.*, 2020. New strategies for vertical transport in chemistry transport models: Application to the case of the Mount Etna eruption on 18 March 2012 with CHIMERE v2017r4. *Geosci. Model Dev.*, 13 (11), 5707-5723. https://doi.org/10.5194/gmd-13-5707-2020

Lapere R., *et al.*, 2021a. Pathways for wintertime deposition of anthropogenic light-absorbing particles on the Central Andes cryosphere. *Environmental Pollution*, 272. https://doi.org/10.1016/j.envpol.2020.115901

Lapere R., *et al.*, 2021b. Seasonal variation in atmospheric pollutants transport in central Chile: Dynamics and consequences. *Atmos. Chem. Phys.*, 21 (8), 6431-6454. https://doi.org/10.5194/acp-21-6431-2021

Lapere R., *et al.*, 2024. Polar aerosol atmospheric rivers: Detection, characteristics, and potential applications. *J. Geophys. Res.: Atmospheres*, 129 (2), e2023JD039606. https://doi.org/10.1029/2023JD039606

Leelossy A., *et al.*, 2016. Eulerian and Lagrangian approaches for modelling of air quality, *In:* Batkai A. *et al.* (ed.), *Mathematical problems in meteorological modelling*, Springer, 73-85. https://doi.org/10.1007/978-3-319-40157-7_5

Liu E.J., *et al.*, 2015. Optimising shape analysis to quantify volcanic ash morphology. *GeoRes. J.*, 814-30. https://doi.org/10.1016/j.grj.2015.09.001

Liu J., *et al.*, 2009. Evaluating inter-continental transport of fine aerosols: (1) Methodology, global aerosol distribution and optical depth. *Atmos. Environ.*, 43 (28), 4327-4338. https://doi.org/10.1016/j.atmosenv.2009.03.054

Long P.K., *et al.*, 2019. Atmospheric transport of 131I and 137Cs from Fukushima by the East Asian northeast monsoon. *Journal of Environmental Radioactivity*, 19774-80. https://doi.org/10.1016/j.jenvrad.2018.12.003

Mailler S., *et al.*, 2024. New explicit formulae for the settling speed of prolate spheroids in the atmosphere: Theoretical background and implementation in aerSett v2.0.2. *Geosci. Model Dev.*, 17, 5641-5655. https://doi.org/10.5194/gmd-17-5641-2024

Mailler S., *et al.*, 2023. aerSett v1.0: A simple and straightforward model for the settling speed of big spherical atmospheric aerosols. *Geosci. Model Dev.*, 16 (3), 1119-1127. https://doi.org/10.5194/gmd-16-1119-2023

Mallios S.A., *et al.*, 2020. Effects of dust particle sphericity and orientation on their gravitational settling in the earth's atmosphere. *J. Aerosol Sci.*, 150, 105634. https://doi.org/10.1016/j.jaerosci.2020.105634

Mallios S.A., *et al.*, 2021. Orientation of non spherical prolate dust particles moving vertically in the Earth's atmosphere. *J. Aerosol Sci.*, 151, 105657. https://doi.org/10.1016/j.jaerosci.2020.105657

Mårtensson E.M., *et al.*, 2003. Laboratory simulations and parameterization of the primary marine aerosol production. *J. Geophys. Res.: Atmospheres*, 108(D9), 4297. https://doi.org/10.1029/2002JD002263

Marticorena B., Bergametti G., 1995. Modeling the atmospheric dust cycle: 1. Design of a soil-derived dust emission scheme. *J. Geophys. Res.: Atmospheres*, 100(D8), 16415-16430. https://doi.org/10.1029/95JD00690

Menut L., *et al*., 2021. Impact of Ragweed Pollen Daily Release Intensity on Long-Range Transport in Western Europe. *Atmosphere*, 12 (6), 693. https://doi.org/10.3390/atmos12060693

Möhler O., *et al*., 2007. Microbiology and atmospheric processes: The role of biological particles in cloud physics. *Biogeosciences*, 4 (6), 1059-1071. https://doi.org/10.5194/bg-4-1059-2007

Moore R.A., *et al*., 2020. Wildland fire as an atmospheric source of viable microbial aerosols and biological ice nucleating particles. *ISME Journal*, 15 (2), 461-472. https://doi.org/10.1038/s41396-020-00788-8

Morrison H., *et al*., 2005. A New Double-Moment Microphysics Parameterization for Application in Cloud and Climate Models. Part I: Description. *J. Atmos. Sci.*, 62, 1665-1677. https://doi.org/10.1175/JAS3446.1

Nabavi S.O., *et al*., 2023. Spatiotemporal variation of radionuclide dispersion from nuclear power plant accidents using FLEXPART mini-ensemble modeling. *Atmos. Chem. Phys.*, 23 (13), 7719-7739. https://doi.org/10.5194/acp-23-7719-2023

Nash D., *et al*., 2018. The role of atmospheric rivers in extratropical and polar hydroclimate. *J. Geophys. Res.: Atmospheres*, 123 (13), 6804-6821. https://doi.org/10.1029/2017JD028130

NOAA/NASA/USAF, 1976. U.S Standard Atmosphere 1976. https://ntrs.nasa.gov/citations/19770009539

Okada K., *et al*., 2001. Shape of atmospheric mineral particles collected in three Chinese arid-regions. *Geophys. Res. Lett.*, 28 (16), 3123-3126. https://doi.org/10.1029/2000gl012798

Olofsson E., 1988. Dispersal of the nuclear polyhedrosis virus of Neodiprion sertifer from soil to pine foliage with dust. *Entomologia Experimentalis et Applicata*, 46 (2), 181-186. https://doi.org/10.1111/j.1570-7458.1988.tb01109.x

Ontiveros V.J., *et al*., 2021. General decline in the diversity of the airborne microbiota under future climatic scenarios. *Sci. Rep.*, 1120223. https://doi.org/10.1038/s41598-021-99223-x

Pereira Freitas G., *et al*., 2023. Regionally sourced bioaerosols drive high-temperature ice nucleating particles in the Arctic. *Nat. Comm.*, 14 (1), 5997. https://doi.org/10.1038/s41467-023-41696-7

Pisso I., *et al*., 2019. The Lagrangian particle dispersion model FLEXPART version 10.4. *Geosci. Model Dev.*, 12 (12), 4955-4997. https://doi.org/10.5194/gmd-12-4955-2019

Plu M., *et al*., 2021. An ensemble of state-of-the-art ash dispersion models: Towards probabilistic forecasts to increase the resilience of air traffic against volcanic éruptions. *Natural Hazards and Earth System Sciences*, 21 (10), 2973-2992. https://doi.org/10.5194/nhess-21-2973-2021

Pope F.D., 2010. Pollen grains are efficient cloud condensation nuclei. *Environ. Res. Lett.*, 5 (4), 44015. https://doi.org/10.1088/1748-9326/5/4/044015

Prata A.T., *et al*., 2021. FALL3D-8.0: A computational model for atmospheric transport and deposition of particles, aerosols and radionuclides. Part 2: Model validation. *Geosci. Model Dev.*, 14 (1), 409-436. https://doi.org/10.5194/gmd-14-409-2021

Prospero J.M., *et al*., 2005. Interhemispheric transport of viable fungi and bacteria from Africa to the Caribbean with soil dust. *Aerobiologia*, 21 (1), 1-19. https://doi.org/10.1007/s10453-004-5872-7

Reche I., *et al*., 2018. Deposition rates of viruses and bacteria above the atmospheric boundary layer. *ISME Journal*, 12 (4), 1154-1162. https://doi.org/10.1038/s41396-017-0042-4

Riley C.M., *et al*., 2003. Quantitative shape measurements of distal volcanic ash. *J. Geophys. Res.: Solid Earth*, 108 (B10). https://doi.org/10.1029/2001jb000818

Saylor R.D., *et al*., 2019. The particle dry deposition component of total deposition from air quality models: Right, wrong or uncertain? *Tellus B: Chemical and Physical Meteorology*, 71 (1), 1550324. https://doi.org/10.1080/16000889.2018.1550324

Schwaiger H.F., *et al*., 2012. Ash3d: A finite-volume, conservative numerical model for ash transport and tephra deposition. *J. Geophys. Res.*, 117 (B4). https://doi.org/10.1029/2011jb008968

Sharma N.K., *et al*., 2007. Airborne algae: Their present status and relevance. *J. Phycol.*, 43 (4), 615-627. https://doi.org/10.1111/j.1529-8817.2007.00373.x

Shields C.A., *et al*., 2018. Atmospheric river tracking method intercomparison project (ARTMIP): Project goals and experimental design. *Geoscientific Model Development*, 11 (6), 2455-2474. https://doi.org/10.5194/gmd-11-2455-2018

Shupe M.D., *et al*., 2022. Overview of the MOSAiC expedition: Atmosphere. *Elementa: Science of the Anthropocene*, 10 (1), 60. https://doi.org/10.1525/elementa.2021.00060

Sprenger M., Wernli H., 2015. The LAGRANTO Lagrangian analysis tool – version 2.0. *Geoscientific Model Development*, 8 (8), 2569-2586. https://doi.org/10.5194/gmd-8-2569-2015

Stein A.F., *et al*., 2015. NOAA s HYSPLIT Atmospheric transport and dispersion modeling system. *Bull. Am. Meteorol. Soc.*, 96 (12), 2059-2077. https://doi.org/10.1175/bams-d-14-00110.1

Stokes G.G., 1851. On the effect of the internal friction of fluids on the motion of pendulums. *Transactions of the Cambridge Philosophical Society*, 9, part II, 8-106. https://www3.nd.edu/~powers/ame.60635/stokes1851.pdf

Subba T., *et al*., 2023. Simulating the transport and rupture of pollen in the atmosphere. *J. Adv. Model. Earth Sy.*, 15 (3). https://doi.org/10.1029/2022ms003329

Sun J., Ariya P.A., 2006. Atmospheric organic and bio-aerosols as cloud condensation nuclei (CCN): A review. *Atmos. Environ.*, 40 (5), 795-820. https://doi.org/10.1016/j.atmosenv.2005.05.052

van der Does M., *et al*., 2018. The mysterious long-range transport of giant mineral dust particles. *Sci. Adv.*, 4 (12). https://doi.org/10.1126/sciadv.aau2768

Van Leuven S., *et al*., 2023. An optimisation method to improve modelling of wet deposition in atmospheric transport models: Applied to FLEXPART v10.4. *Geoscientific Model Development*, 16 (18), 5323-5338. https://doi.org/10.5194/GMD-16-5323-2023

Vida M., *et al*., 2024. Modelling of atmospheric concentrations of fungal spores: A 2-year simulation over France using CHIMERE. *Atmos. Chem. Phys.*, 18, 10601-10615. https://doi.org/10.5194/acp-24-10601-2024

Vignati E., *et al*., 2010. Global scale emission and distribution of sea-spray aerosol: Sea-salt and organic enrichment. *Atmos. Environ.*, 44 (5), 670-677. https://doi.org/10.1016/j.atmosenv.2009.11.013

Wang X., *et al*., 2014. Development of a new semi-empirical parameterization for below-cloud scavenging of size-resolved aerosol particles by both rain and snow. *Geosci. Model Dev.*, 7, 799-819. https://doi.org/10.5194/gmd-7-799-2014

Werner M., *et al*., 2021. Extension of WRF-Chem for birch pollen modelling—a case study for Poland. *Int. J. Biometeorol.*, 65 (4), 513-526. https://doi.org/10.1007/s00484-020-02045-1

Wille J.D., *et al*., 2019. West Antarctic surface melt triggered by atmospheric rivers. *Nature Geoscience*, 12 (11), 911-916. https://doi.org/10.1038/s41561-019-0460-1

Willis P., Tattelman P., 1989. Drop-size distributions associated with intense rainfall. *J. Appl. Meteorol.*, 283-15. https://doi.org/10.1175/1520-0450(1989)028<0003:DSDAWI>2.0.CO;2

Wilson L., Huang T.C., 1979. The influence of shape on the atmospheric settling velocity of volcanic ash particles. *Earth Planet Sc. Lett.*, 44 (2), 311-324. https://doi.org/10.1016/0012-821x(79)90179-1

Wohltmann I., *et al*., 2010. The Lagrangian chemistry and transport model ATLAS: Simulation and validation of stratospheric chemistry and ozone loss in the winter 1999/2000. *Geoscientific Model Development*, 3 (2), 585-601. https://doi.org/10.5194/GMD-3-585-2010

Yang W., *et al*., 2013. Shape-induced gravitational sorting of Saharan dust during transatlantic voyage: Evidence from CALIOP lidar depolarization measurements. *Geophys. Res. Lett.*, 40 (12), 3281-3286. https://doi.org/10.1002/grl.50603

Zhang L., *et al*., 2001. A size-segregated particle dry deposition scheme for an atmospheric aerosol module. *Atmos. Environ.*, 35, 549-560. https://doi.org/10.1016/S1352-2310(00)00326-5

Zhu Y., Newell R.E., 1998. A proposed algorithm for moisture fluxes from atmospheric rivers. *Monthly Weather Review*, 126 (3), 725-735. https://doi.org/10.1175/1520-0493(1998)126<0725:APAFMF>2.0.CO;2

Section 2

The travel diaries of microorganisms and insects that ride the winds

Chapter 5

Uncovering microbial resilience aloft: Exploring boundary conditions in atmospheric environments

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The survival and potential activity of airborne microbes in the free troposphere and even stratosphere raise intriguing scientific questions with implications for understanding the role of microbes in global environmental processes. This chapter reviews environmental and laboratory studies investigating the parameters and conditions that constrain the boundaries for a living microbial atmosphere, and identifies knowledge gaps that future research could address to better define microbial life aloft.

Environmental investigations of air in the human environment, the broader troposphere, and even the stratosphere have examined the presence and activity of microorganisms in various atmospheric compartments, including ambient air, fog, ice, and cloud water. For recent reviews, see Amato *et al.* (2023), Archer and Pointing (2020), Dassarma *et al.* (2020), Lappan *et al.* (2024), Šantl-Temkiv *et al.* (2022), Tignat-Perrier *et al.*, (2020) and Zhao *et al.* (2022). Active microbes in clouds, for instance, drive significant biogeochemical change on a global scale (see Chapter 6). However, microbial activity in the air outside of water droplets is less well studied, and its global significance is poorly understood. Similarly, the interplay between concurrent complex multiphase abiotic chemical reactions and microbial activity in the atmosphere beyond cloud water, fog, or rain has received little attention.

Aerial environments present a double-edged sword for microorganisms. Stressors such as ultraviolet (UV) radiation, drying conditions, chemical radicals, and electrostatic fields challenge microorganism survival. Yet, these same environments supply oxygen, moisture, nutrients, organic compounds, and even physical protection, that are known to support or enhance microbial growth and survival. In the stratosphere, for example, a combination of desiccative conditions and short-wave UV (UVC) radiation is expected to limit microbial survival beyond approximately 30 km altitude, yet this region offers a natural laboratory to study the effects of UVC and other stressors on microorganism survival (Bryan *et al.*, 2019).

Aerobiology studies have explored the transmission, infectivity, and survival of airborne microbes, or bioaerosols, using rotating drums (used to achieve longer microorganism suspension times) and other types of environmental chambers

(Haddrell and Thomas, 2017; Santarpia *et al.*, 2020). There is a long history of monitoring the viability, culturability, and activity of microbes in simulated atmospheric environments, including water droplets or air (Dillon *et al.*, 2022; Dimmick *et al.*, 1979a; Dimmick *et al.*, 1975; Dimmick *et al.*, 1979b; Goldberg *et al.*, 1958; Hasegawa *et al.*, 2011; Hernandez, 1999; Krumins *et al.*, 2008; Krumins *et al.*, 2014; Šantl-Temkiv *et al.*, 2013; Sattler *et al.*, 2001; Straat *et al.*, 1977); some of the most intriguing experiments were performed in the 1970s, after rotating drums were introduced.

Despite these efforts, significant unknowns persist. Factors influencing microbial survival in the atmosphere, termed "open-air factors" (Druett and May, 1968; Druett and Packman, 1968), have been examined in laboratory studies (Pan *et al.*, 2021), but these studies often fail to replicate the full complexity and concentrations of open-air factors present in the atmosphere. Moreover, with public health concerns driving extensive research on inactivating airborne microorganisms to control the spread of human diseases or improve indoor air quality (Kompatscher *et al.*, 2023), far less attention has been paid to how microbes might thrive in the free troposphere and stratosphere. This chapter synthesizes the literature on key survival enhancers, including substrates and nutrients, and the chemical and physical stressors that may modulate microorganism survival in the atmosphere, detailing their effects in the sections below (see Table 5.1 for an overview of parameters). The conditions described in this chapter can be contrasted with those first experienced by bioaerosols released from water surfaces as described in Chapter 7. By bridging data from environmental observations and controlled experiments, we aim to illuminate microbial resilience aloft, outside of water droplets, and highlight avenues for future exploration.

⏩ Tools for experimental aerobiology

Due to our limited ability to conduct observations and experiments above the planetary boundary layer, laboratory studies must be conducted to examine the effect of atmospheric conditions on airborne microbes. Although field sampling and characterization of *in situ* bioaerosols are important, a deeper mechanistic understanding of such processes could be gained by employing the tools of experimental aerobiology. Many of the same tools of bioaerosol field sampling are used in experimental aerobiology, but the generation of bioaerosols and their containment in a lab are unique aspects of laboratory studies. Commonly used methods to aerosolize biological materials have been detailed in the literature (Alsved *et al.*, 2020), and the main methods mimic natural bioaerosol releasing mechanisms. For example, bubble-bursting in aquatic systems is one of the primary mechanisms by which bioaerosols are generated in nature, and a device to mimic this was designed for laboratory studies (Mainelis *et al.*, 2005). Other methods used to aerosolize biological materials contained in liquid include nebulization, electrospraying, and vibration (Alsved *et al.*, 2020). The choice of aerosolization method will impact the particle size distribution and the viability of the generated bioaerosols (Alsved *et al.*, 2020). Arguably, the most commonly employed aerosol generator is a Collison nebulizer. Although it produces bioaerosols with great efficiency, the continuing impaction of biological particles onto the container walls during liquid recirculation damages them and may result in aerosols that are not representative of the physicochemical properties of bioaerosols present in the environment (Zhen *et al.*, 2014).

Damage could be reduced by using polycarbonate containers instead of glass (Zhen *et al.*, 2014). Aerosol generators that do not recirculate materials (e.g., single-pass devices) are typically better at preserving the integrity of biological samples, but many of them produce lower microorganism concentrations (Krumins *et al.*, 2014; Zhen *et al.*, 2014). Thus, for a given experiment, the bioaerosol concentration and viability must be considered.

To keep biological samples aloft under laboratory conditions, various systems have been used, including static chambers, wind tunnels, rotating chambers/drums, microthread systems, *in situ* aerosol systems, and, more recently, single particle levitation systems (Santarpia *et al.*, 2020). Each can be used to pursue answers to different questions. For example, wind tunnels are useful for understanding the immediate effect of aerosolization on microbe survival, but a rotating chamber is more useful for investigating how time aloft affects microbes (Goldberg *et al.*, 1958; Krumins *et al.*, 2008) over hours and even days. On the other hand, experiments in large chambers are easier to conduct than experiments with rotating drums and enable time scales of hours.

When single-droplet resolution is required, a levitation system, such as "Controlled Electrodynamic Levitation and Extraction of Bioaerosols onto a Substrate" (CELEBS) (Oswin *et al.*, 2022), could be used. Such a system provides insights into the biophysicochemical properties of bioaerosols at short time scales (e.g., seconds) and provides unprecedented understanding of the dynamics of a single bioaerosol particle. Each method for bioaerosol generation and containment has advantages and disadvantages, thus laboratory tools must be employed appropriately to address a specific question about the aerobiome.

Once bioaerosols are generated and introduced into a containment system, environmental variables (open air factors), such as temperature, relative humidity (RH), UV radiation, and particulate matter (PM) concentrations, can be varied to gain an understanding of how bioaerosols function/change when exposed to the dynamic conditions of the atmosphere. The use of these tools to simulate atmospheric conditions for bioaerosols in the laboratory advances the field of aerobiology.

⏩ Growth enhancing compounds in the atmosphere

The presence of microbial growth enhancers (Table 5.1) including energy sources (substrates), carbon sources (organic and inorganic) and nutrients (e.g., N and P), along with adequate humidity, and oxygen as a terminal electron acceptor, could allow microbes in air not only to survive, but also to be metabolically active and even grow. Among potential microbial substrates, the volatile organic compounds (VOCs) have been widely analyzed in both indoor and outdoor air. Atmospheric VOCs are categorized as methane, non-methane VOCs (NMVOCs); natural VOCs (NVOCs), anthropogenic VOCs (AVOCs), and biogenic (BVOCs) (Duan *et al.*, 2023). VOCs exhibit substantial geographical, temporal, and seasonal variability in the atmosphere. Non-volatile organic compounds such as sugars are also released into the atmosphere, primarily through combustion. Nutrients such as the N-source, ammonia, and total phosphorus, have also been measured in the natural atmospheric environment (Table 5.1).

Table 5.1. Atmospheric environmental concentrations and levels of chemical and physical stressors and growth enhancers affecting microorganisms aloft.

Parameter	Location	Value/Range	Time frame	Notes	Reference
		Growth substrates and nutrients			
Methane	Michigan, USA 8 landfills	3.94 ppm (mean of 66 samples) 38 ppm (maximum)	May 2019 - September 2021		Xia *et al.*, 2023
	USA, locations not identified 4 landfills	6 to 71 ppmv	2020 and 2022		Abichou *et al.*, 2023
	Global atmosphere	1.93191 ppm globally averaged	2024	Monthly mean marine surface sites	Lan *et al.*, 2024
	Permian Basin Texas, USA Texas-New Mexico, USA Border	2 – 4 ppm	July-August 2022		Chulakadabba *et al.*, 2023
	Paris, France	43 – 2700 ppb	September 2018 - March 2019	Methane enhancement above background	Defratyka *et al.*, 2021
	Los Angeles, California, USA	up to >10 ppm	2016-2019	Urban hotspots	Okorn *et al.*, 2021
	West coast of Turkmenistan	up to 14 ppm	2017-2020	XCH_4, average air column concentration	Irakulis-Loitxate *et al.*, 2022
	Coal mine ventilation air, global	1 to 5% methane 10,000 – 50,000 ppm		General ventilation air targets for the coal mining industry	Schultz *et al.*, 2003
Isoprene	China	0.35 ± 0.03 ppbv	2012-2014	20 geographically distinct sites	Zhang *et al.*, 2020
Ethene	Austrian Alps, Tyrol, Austria	1.4 – 9.9 ppbv	April, July, August, 2001 May 2002	Valley and mountain top	Smidt *et al.*, 2005

Parameter	Location	Value/Range	Time frame	Notes	Reference
Ethene	Manitou Experimental Forest Observatory, Central Rocky Mountains, USA	318 ppt median (153 ppt, 10th percentile; 574 ppt 90th percentile)	June-August 2014		Rhew *et al.*, 2017
	Nainital, India Central Himalayas	0.40 ± 0.24 ppbv	January 2017 - December 2020	Winter (pristine)	Rajwar *et al.*, 2024
	Haldwani, India Indo-Gangetic Plain	1.84 ± 1.34 ppbv	January 2017 - December 2020	Winter (urban)	
	Phoenix, Arizona, USA	260 ± 190 pptv (low)	August-September 1999-2005	Measurements from 28 cities; low and high values are shown	Baker *et al.*, 2008
	Los Angeles, California, USA	2,430 ± 1,360 pptv (high)	August-September 1999-2005		
	Mexico City, Mexico	up to 68 ppbv	November 1999 and March 2000		Altuzar and Arriaga, 2005
	Houston, Texas, USA	<0.7 ppbv – 69 ppbv	September 2006		De Gouw *et al.*, 2009
	Pearl River Delta, China	33-10,530 pptv	August 2001 - December 2002	187 air samples	Guo *et al.*, 2006
Ethanol	Wilmington, North Carolina, USA	0.78 ± 0.33 ppbv	July 2011		Willey, 2019
	Wilmington, North Carolina, USA	3.91 ± 2.58 ppbv	July 2016		
	Los Angeles, California, USA	9 ± 5 ppbv	May-June 2010		De Gouw, 2012
	Troposphere Pacific Ocean	~20 – 80 ppt	February-March 1994		Singh *et al.*, 1995
	Outdoor air, various locations	0.24 – 176 ppb			Nazaroff and Weschler (2024) and references therein
	Indoor air, various locations	11.1 – 630 ppb			

Table 5.1. (continued)

Parameter	Location	Value/Range	Time frame	Notes	Reference
Ethanol	Porto Alegre, Brazil	0.4 – 68.2 ppbv	1996-1997	Urban air	Grosjean *et al.*, 1998
	Arizona, USA	0.4 – 2.6 ppbv	February-September 1982	Rural and urban air	Snider and Dawson, 1985
	São Paulo, Brazil	176.3 ± 38.1 ppbv	February 1998	Urban air	Nguyen *et al.*, 2001
Acetic Acid	Remote and marine areas, various locations	0.05 – 8 ppbv			Khare *et al.* (1999) and references therein
	Urban areas, various locations	0.2 – 17.8 ppbv			
	Over burning biomass, various locations	3,000 – 5,000 x 10^3 ppt			
	Outdoor air, various locations	0.04 – 16 ppb			Nazaroff and Weschler (2020) and references therein
	Indoor air, various locations	4.3 – 53 ppb			
Glucose	Victoria Land, Antarctica	86 pg/m^3 – 1,356 pg/m^3	November 2010 - January 2011	PM_{10} aerosols	Barbaro *et al.*, 2015
	Howland Experimental Forest, Maine, USA	3.1 – 50 ng/m^3	May-October 2002	Above canopy, 30 m	Medeiros *et al.*, 2006
	France	0.1 – 297.2 ng/m^3 20.4 ± 15.6 ng/m^3	2011-2017	28 sites PM_{10}	Samaké *et al.*, 2019a
	Santiago, Chile	10 – 2,210 ng/m^3 (mean = 940 ng/m^3)	Winter 1991	Total suspended particles	Simoneit *et al.*, 2004
	Datong, China	102 ng/m^3	April 1991	Total suspended particles	
	Rondônia, Brazil pasture site	13.9 – 62.1 ng/m^3	September-October 1999	5 m above ground level	Graham *et al.*, 2002
	Rondônia, Brazil forest site	4.6 – 40.9 ng/m^3	September-October 1999	50 m above ground level	

Parameter	Location	Value/Range	Time frame	Notes	Reference
Ammonia	Seoul, Korea	10.9 ± 4.25 ppb 12.3 ± 4.23 ppb	September 2010 - August 2011		Phan *et al.*, 2013
	Remote continental and oceanic areas	<1 ppbv			Nair and Yu (2020) and references therein
	Intensive agriculture	>24 ppbv			
	Beijing, China	1.2 – 66.9 μg/m^3	2020-2021		Gu *et al.*, 2022
Total Phosphorus	Various outdoor locations	2 – 200 ng/m^3			Mahowald *et al.* (2008) and references therein
	Western North Atlantic, Bermuda	0.6 – 21.9 ng/m^3	1974, 1975		Graham and Duce, 1982
Chemical Factors					
pH	Beijing, China	4.5 ± 0.7	Winter 2016-2017	$PM_{2.5}$ average	Ding *et al.*, 2019
		4.4 ± 1.2	Spring 2016-2017		
		4.3 ± 0.8	Autumn 2016-2017		
		3.8 ± 1.2	Summer 2016-2017		
	Ann Arbor, USA	3.5	August 2016	0.4-2.5 μm particles	Craig *et al.*, 2018
		3	August 2016	>2.5 μm particles	
	Po Valley, Italy	3.9 ± 0.8	Winter 2012, 2013		Masiol *et al.*, 2020
		2.2 ± 0.5	Summer 2012		
	São Paulo, Brazil	4.2 – 5.2	Winter 2012	Coarse particle mode	Vieira-Filho *et al.*, 2016
	Southern Ocean	1.4	January-February 2015		Dall'osto *et al.*, 2019
Ozone	Cincinnati, Ohio, USA metropolitan area	2.88 – 60.46 ppb	March-October 2002 and 2003	Daily average	Adhikari *et al.*, 2006

Table 5.1. (continued)

Parameter	Location	Value/Range	Time frame	Notes	Reference
Ozone	Rural areas, UK	70.8 – 92.2 ppb	1992-2019		Diaz *et al.*, 2020
	Urban areas, UK	65.0 – 81.7 ppb			
	Valdejero Natural Park, Spain	68.3 – 83.2 μg/m^3	June, July, August 2009-2018	Yearly average	Gómez *et al.*, 2020
	Košetice, Czech Republic	64.7 μg/m^3	2015-2021 (daily average)	2 m above ground level	Hůnová *et al.*, 2023
		65.4 μg/m^3		8 m	
		71.5 μg/m^3		50 m	
		79.3 μg/m^3		230 m	
	Urban areas, Uganda	32.59 – 82.69 μg/m^3	December 2018 - May 2020	2-month average	Okure *et al.*, 2022
	Tehran, Iran	17.1 – 25.1 ppb	January 2021 - December 2021		Borhani *et al.*, 2023
	Atlantic West Coast, Ireland	69 – 75 μg/m^3	2015-2019		Mchugh *et al.*, 2023
	Urban areas, Ireland	39 – 43 μg/m^3			
	New South Wales, Australia	36 – 39 ppb	2018-2020	Average from continental air masses	Riley *et al.*, 2022
		14 – 30 ppb		Average from marine air masses	
	Mt. Tai, China	74.53 ± 12.06 ppb	May-June 2019	1534 m a.s.l.	Ye *et al.*, 2021
	Tai'an City, China	58.28 ± 30.46 ppb	May-July 2018	10 km away from the Mt. Tai base	

Parameter	Location	Value/Range	Time frame	Notes	Reference
H_2O_2	Mt. Mitchell, USA	0.1 – >4 ppbv	May-September 1988		Claiborn and Aneja, 1991
	Whiteface Mt., USA	0.15 – 5.15 ppbv	July 1995		Balasubramanian and Husain, 1997
	North China Plain, China	0.51 ± 0.90 ppbv	June-July 2014	24-hour average	Wang *et al.*, 2016
	Tai'an City, China	0.93 ± 1.01 ppbv	May-July 2018	10 km away from the Mt. Tai base	Ye *et al.*, 2021
	Mt. Tai, China	2.05 ± 1.20 ppbv	May-June 2019	1534 m a.s.l.	
OH Radicals	Chengdu, China	1.6 – 15.9 × 10^6 molecules/cm^3	August-September 2019	Daily peak concentrations	Zhang *et al.*, 2022
		<1 × 10^6 molecules/cm^3		Nighttime concentration	
	Suriname rainforest	0.25 – 0.75 ppt	October 2005	0-8 km a.s.l.	Martinez *et al.*, 2010
	South Atlantic Ocean	0.3 pptv	March 2007	Daily maximum	Beygi *et al.*, 2011
	Gulf of Aden, Arabian Sea	0.8 pptv	June-September 2017	Daily maximum	Dienhart *et al.*, 2021
	Coastal region near Norfolk, UK	2.6 – 17 × 10^6 molecules/cm^3	July 2015	Daily maximum	Woodward-Massey *et al.*, 2023
Metals					
Zn	Henan Province, China	19.9 – 252.9 μg/m^3	December 2020, April-May 2021, August-September 2021	$PM_{2.5}$	Zhang *et al.*, 2024
Fe	Henan Province, China	10.3 – 109.4 μg/m^3			
Zn	Panzihua, China	14.9 ± 3.6 ng/m^3	April 2017, July 2017, October 2017, January 2018	PM_{10} median concentration	Wang *et al.*, 2020
Fe	Beijing, China	4,528.2 ± 434.1 ng/m^3	December 2006	PM_{10}, polluted episode	Tan *et al.*, 2016
Cu	Beijing, China	71 ± 29.4 ng/m^3			
Zn	Beijing, China	502.1 ± 184.4 ng/m^3			

Table 5.1. (continued)

Parameter	Location	Value/Range	Time frame	Notes	Reference
Fe	Southeast Atlantic Ocean	<25 – 2,438 pmol/m^3	October 2004, May 2005, November 2005, February-March 2008, October-November 2010, December 2011 - January 2012		Chance *et al.*, 2015
Zn	Southeast Atlantic Ocean	<3 – 92 pmol/m^3			
Cu	La Esperanza	0.13 µg/m^3	February-March 1989 (dry season) September-November 1988 (rainy season)	Rural savanna sites: Average in dry season Average in rainy season	Morales *et al.*, 1996
	Catatumbo, Venezuela	0.35 µg/m^3			
Salt (Na^+)	La Esperanza	1.7 µg/m^3			
	Venezuela	0.61 µg/m^3			
	Catatumbo, Venezuela	0.87 µg/m^3			
		0.42 µg/m^3			
	Beijing, China	2.36 µg/m^3	December 2006	$PM_{2.5}$	Tan *et al.*, 2016
		3.13 µg/m^3		PM_{10}	
	Snowy Mountains, Australia	178 ng/m^3	July 2013 - July 2017	1,287 m a.s.l. Yearly average	Tadros *et al.*, 2018
	Cape Grim, Tasmania, Australia	1,009 ng/m^3	April 1998 - June 2016	Yearly average Remote coastal site	
Physical Factors: Electrostatic charge	Lahemaa National Park, Estonia	Mean charge magnitude 21-981 elementary charges	Järvselja in 1973, Tammistu in 1974, and Koke in 1978	128 spore samples of 31 species of Agaricomycetes collected	Saar and Salm, 2014
	Indoor and outdoor environments; Peking, China	21–29 elementary charge units outdoors; 46–92 elementary charge units indoors	Winter of 2012		Wei *et al.*, 2014

Growth in the atmosphere outside water droplets has not been directly assessed by examining cell division in natural air due to the many difficulties such a study would present. However, it is not surprising, given the presence of potential metabolic enhancers, that microbes in the atmosphere exhibit physiological characteristics that suggest they are metabolically active (Amato *et al.*, 2017; Erkorkmaz *et al.*, 2023; Klein *et al.*, 2016; Liu *et al.*, 2020; Šantl-Temkiv *et al.*, 2018). The ribosomal RNA content (i.e., number of 16S rRNA molecules detected) of specific microbial taxa collected from the boundary layer over southwest Greenland indicated active bacteria from the phylum Actinobacteria (e.g., subclass Rubrobacteridae), and increased ribosomal content was positively correlated with water vapor pressure (Šantl-Temkiv *et al.*, 2018). Further, a comparison of metatranscriptomes of microbial assemblages from clear air and clouds from Puy de Dôme Mountain, France, suggests that activity and growth may occur both inside and outside of water droplets, however, to a far greater degree in cloudwater (Péguilhan *et al.*, 2024).

Direct assessment of the metabolic activity and growth of aerosolized bacteria in the presence of growth enhancers has been examined in a handful of studies using laboratory aerosolization chambers (Dillon *et al.*, 2022; Dimmick *et al.*, 1979a; Dimmick *et al.*, 1975; Dimmick *et al.*, 1979b; Hernandez, 1999; Krumins *et al.*, 2014; Peccia and Hernandez, 2001). Far more studies have examined microbial persistence and resistance by examination of cultivability after aerosolization and exposure to stressors (Table 5.2) or other conditions. These studies generally included aerosolization from a buffered solution without soluble carbon/energy sources present and without intentional addition of volatile substrates –in short, with no intention of enhancing growth. Even so, a few of these studies of survival noted that growth enhancers were indeed incorporated unintentionally, e.g. through prior disinfection of chambers using alcohol (Hasegawa *et al.*, 2011), use of spent medium or aerosolization of cells as clusters (Dybwad and Skogan, 2017), and possibly presence of VOCs and reactive nitrogen sources (other than N_2) in the air used for cultivation (Schmider *et al.*, 2024).

Notably, studies on survival of airborne viruses focused primarily on the fate of viral particles (see subsequent sections). However, one early study used airborne *Escherichia coli* infected by coliphage T7 to examine if bioaerosols collected at various time points would support phage growth and lysis versus cell growth/colony formation after collection, thus distinguishing between modes of activity loss (Cox and Baldwin, 1964).

Here, we review a few selected growth substrates and nutrients in air (Table 5.1) and their potential impacts on bacterial activity, with a focus on those that have been correspondingly used in aerobiology experiments.

Methane

Global emissions of methane from 2008 to 2017 were estimated to be 576 Tg/yr (Saunois *et al.*, 2020) and by 2024, the concentration in the atmosphere had reached *circa* 1.93 ppm globally (Lan *et al.*, 2024) (Table 5.1). Atmospheric methane has increased rapidly through methanogenic activity related to agriculture, landfills, termites, and wetlands (Kirschke *et al.*, 2013), and through the increased extraction of natural gas (Caulton *et al.*, 2014). Permafrost thaw resulting from global warming is predicted to be an increasing source of methane to the atmosphere (Olefeldt *et al.*, 2013), depending

upon local hydrologic conditions (Bruhwiler *et al.*, 2021; Oh *et al.*, 2020), with evidence suggesting that emissions are increasing from perennially thawed soils in permafrost (Walter Anthony *et al.*, 2024).

Methane has a half-life of 8 to 9 years in the atmosphere (Masson-Delmotte *et al.*, 2021) and is removed primarily by chemical reaction with the OH radical (Prather *et al.*, 2012), with other atmospheric and ocean boundary removal processes having a lesser impact (Kirschke *et al.*, 2013). While physical-chemical removal processes dominate, methane also has a biological sink as a carbon and energy source for methanotrophic bacteria in soils, aqueous environments, and the phyllosphere (Hanson and Hanson, 1996). Methanotrophs suspended in the aerial environment would be primarily exposed to the prevailing aerial methane concentration of 1.93 ppm. However, there are also numerous methane hotspots near the Earth's surface.

Human-built infrastructure (e.g., energy infrastructure, waste management, etc.) is a source of higher concentrations of methane in the atmosphere and the formation of hotspots (Table 5.1). A survey of leakages in Paris, France (Defratyka *et al.*, 2021) measured methane concentration enhancements over background levels in ambient air from 43 to 2700 ppb, with a measurement from a boiler room vent showing an enhancement as high as 40 ppm. Methane concentrations in the air in Los Angeles (Okorn *et al.*, 2021) transiently reached as high as 10 ppm in areas near oil and gas activity.

Municipal waste management landfills host anaerobic methanogenic archaea and represent another substantial methane emitter (Mønster *et al.*, 2019; Weaver *et al.*, 2019). Eight landfills in southeast Michigan, USA, were surveyed to determine methane concentrations in the air near these facilities. An average methane concentration of 3.94 ppm was observed, with a peak maximum reading of 38 ppm (Table 5.1), indicating areas where airborne microbes could have access to far higher methane levels than background levels suggest (Xia *et al.*, 2023). A survey of four other US landfills for methane concentrations in the air and thousands of ground and drone-based measurements yielded average concentrations of 6 to 71 ppm (Abichou *et al.*, 2023) (Table 5.1).

Measuring methane in the atmosphere is highly focused on finding hotspots of methane emissions that could lead to better global estimates of the methane budget and targeted mitigation of such emissions to slow climate change. Remote sensing of methane is increasingly available and generally provides the dry-air mixing ratio of methane (XCH_4), which is the average amount of methane in a vertical air column above a specific location, excluding water vapor (part per billion or ppb) (Jacob *et al.*, 2022). Increasing use of remote sensing to find areas of high methane emissions raises the intriguing possibility of also locating potential hotspots of methanotrophic activity in the air.

Imaging spectrometers MethaneSAT, a satellite instrument, and MethaneAIR, an aircraft-borne instrument, showed enhancement of methane by 2 to 4 ppm over background via emissions from coal bed methane and natural gas operations in the Permian Basin, USA (Chulakadabba *et al.*, 2023). The west coast of Turkmenistan, which has been identified as one of the largest methane hotspots in the world (Irakulis-Loitxate *et al.*, 2022) had transient XCH_4 concentrations of up to 14,000 ppm. Other known point sources are coal mines worldwide, which routinely emit mine ventilation gas that is maintained to be less than the explosive limit of methane (<5% or 50,000 ppm), but more typically at <1% methane or 10,000 ppm (Schultz *et al.*, 2003) (Table 5.1).

From the environmental data it appears that methanotrophic bacteria aloft in the atmosphere could be exposed to methane concentrations from near the atmospheric concentration of 1.93 ppm to as high as 50,000 ppm, transiently (Table 5.1). Methanotrophic bacteria oxidize methane under aerobic conditions and have traditionally been classified as those with either a high affinity or a low affinity for methane (Bender and Conrad, 1992; Knief and Dunfield, 2005). High-affinity methanotrophs oxidize methane at atmospheric concentrations and have been found in soils exposed to the atmosphere as the main source of methane, while low-affinity methanotrophs were more often found in soils near interfaces with zones of microbial methanogenesis or natural gas deposits, for example (Bender and Conrad, 1992). Low-affinity methanotrophs oxidize methane at atmospheric concentrations and slower rates, while high-affinity methanotrophs oxidize methane at higher concentrations and faster rates (Knief and Dunfield, 2005). Methanotrophs thus could have different potential useful applications in mitigating methane as a greenhouse gas (Lidstrom, 2024). Recently, Schmider *et al.* (2024) have cultivated methanotrophic colonies on floating filters with methane supplied in the headspace at atmospheric concentrations. They reported that the traditional divisions may not neatly hold and that a variety of methanotrophic strains, including those previously known as low-affinity methanotrophs, can shift physiology to actively metabolize atmospheric methane concentrations and even incorporate N from the atmosphere to support growth (Schmider *et al.*, 2024). Their findings suggest that a variety of methanotrophs may be uniquely adapted to live in the air with atmospheric methane concentrations. At the other end of the concentration range, soil methanotrophs degraded methane at up to 19,000 ppmv in the headspace, indicating the potential for atmospheric hotspots of methane to also support aerial methanotrophic activity (Henckel *et al.*, 2000).

A single environmental study of the atmosphere showed the presence and potential activity of methanotrophs in rain and air collected over a landfill. Methanotrophic enrichments from the air and rain samples were active under cloud-like conditions and at atmospheric methane concentrations when cultivated in liquid medium (Šantl-Temkiv *et al.*, 2013), suggesting they could also be active in the atmosphere. Growth of airborne bacteria on methane outside water droplets remains limited (Table 5.2). Methanotrophic enrichment cultures from leaf and bioaerosol sources were aerosolized into rotating gas-phase bioreactors in the presence of 1,500 ppmv methane, a value between atmospheric and coal mine concentrations (Dillon *et al.*, 2022). Growth was shown in three of seven experiments, which was demonstrated by ^{13}C incorporation from ^{13}C-labeled methane into DNA via stable isotope probing (Radajewski *et al.*, 2000). Airborne microbial growth appeared to be related to higher humidities in the air. Thus, there is a possibility that airborne methanotrophs can incorporate methane to maintain their viability both at lower and higher prevailing concentrations, given an appropriate humidity.

Non-methane volatile organic compounds

Global NMVOC (Non-Methane Volatile Organic Compounds) emissions from 1991 to 2017 included emissions of AVOCs of 139-163 TgC/yr and of BVOCs of 424-591 TgC/yr (Duan *et al.*, 2023). BVOCs are largely made up of terpenoids, including dominant isoprene, and are emitted from plants and photosynthetic microalgae

(Sindelarova *et al.*, 2022). Ethene, ethanol, methanol, and acetone are also substantial constituents of BVOCs (Sindelarova *et al.*, 2022). AVOCs include acids, alcohols, alkanes, alkenes, aromatics, and chlorinated hydrocarbons, among other constituents (Duan *et al.*, 2023). These compounds undergo a variety of abiotic reactions in the atmosphere, leading to half-lives that vary from minutes to days (Koppmann, 2020). Many of these VOCs however, also serve as carbon and energy sources for microorganisms, and there is some evidence that they may serve in this way in the atmospheric environment (Amato *et al.*, 2017; Dillon *et al.*, 2022; Krumins *et al.*, 2014). Specific concentrations in air, which would be present as microbial substrates, have been reported for a variety of NMVOCs (Table 5.1).

Isoprene is the dominant BVOC with a production of ~594 TgC/yr (Koppmann, 2020; Sindelarova *et al.*, 2022) and prevailing concentrations in the atmosphere range from tenths of a ppb on average, and transiently at the ppb level in urban areas (Wagner and Kuttler, 2014) because of anthropogenic sources (Table 5.1). The metabolism of isoprene by microorganisms occurs in marine environments (Alvarez *et al.*, 2009) and soils (Cleveland and Yavitt, 1998) and by soil isolates (Van Ginkel *et al.*, 1987), and is a major sink for isoprene in the environment (Mcgenity *et al.*, 2018).

Ethene is both a biogenic and an anthropogenic volatile gas (Sawada and Totsuka, 1986) emitted to the atmosphere at 19.2 to 23.5 Tg/yr (Sindelarova *et al.*, 2022). It is present at a fraction of ppbv levels in pristine forested areas of Earth's near atmosphere (Rajwar *et al.*, 2024; Rhew *et al.*, 2017; Smidt *et al.*, 2005) but is transiently emitted and observed at higher levels (up to 69 ppbv) in urban areas where it is produced and released through combustion, industrial, or refining activities (Altuzar *et al.*, 2005; Baker *et al.*, 2008; De Gouw *et al.*, 2009; Guo *et al.*, 2006) (Table 5.1). Ethene is metabolized under aerobic conditions by bacteria that have been isolated from a variety of soil and groundwater environments (De Bont and Albers, 1976; Mattes *et al.*, 2005; Van Ginkel *et al.*, 1987; Verce *et al.*, 2001).

Ethanol enters the atmosphere at an estimated 25-56 Tg/yr through emissions from plants, biomass decay and burning, atmospheric reactions, and anthropogenic production (Kirstine and Galbally, 2012). Concentrations in the atmosphere were 80 ppt in the upper troposphere over the Pacific Ocean (Singh *et al.*, 1995), while levels in urban and rural air ranged from 0.4 and 2.6 ppbv at rural and urban Arizona, USA locations, respectively (Snider and Dawson, 1985). Concentrations as high as 176.3 ± 38.1 ppbv were observed in Sao Paulo, Brazil (Nguyen *et al.*, 2001), a location with high use of ethanol-based vehicle fuels. Even higher concentrations (630 ppbv) are found in indoor air (Nazaroff and Weschler, 2024) (Table 5.1). Vapor phase ethanol released to air near distilleries and in wine cellars, called the "angels' share", could reach higher concentrations, and it is well known for supporting fungal growth on nearby surfaces (Ing *et al.*, 2018; Tribe *et al.*, 2006). Vapor phase concentrations of 0.1 to 10 ppm ethanol supported germination of *Baudoinia compniacensis* isolated from such surfaces, while 100 ppm suppressed germination (Ewaze *et al.*, 2008).

Acetic acid sources to the atmosphere are not entirely defined but are thought to come primarily from photochemically induced reactions with isoprene and monoterpenes in the atmosphere, vegetation, and biomass burning, and to a lesser extent, vehicular emissions and direct biogenic emissions (Franco *et al.*, 2020; Khare *et al.*, 1999). Acetic acid concentrations in the gas phase have been reviewed extensively and are reported

to range from tenths of a ppbv in remote locations up to 17.6 ppbv in urban areas, and 5000 ppbv directly over burning biomass (Khare *et al.*, 1999). A review of indoor and outdoor acetic acid concentrations indicated 16 ppb indoors and 53 ppb outdoors, as high concentrations (Nazaroff and Weschler, 2020) (Table 5.1).

Laboratory studies to determine if airborne microbes outside water droplets have enhanced activity in the presence of NMVOCs are rare (Table 5.2). To the best of our knowledge, there are no laboratory studies of airborne bacteria in the presence of isoprene; however, a *Pseudomonas syringae* strain isolated from rain had the ability to produce isoprene during growth on acetate (Ling *et al.*, 2021), suggesting a potential bioatmospheric source of isoprene. Increases in airborne *Xanthobacter autotrophicus* (Van Ginkel and De Bont, 1986) cells aerosolized into gas-phase rotating bioreactors (Goldberg *et al.*, 1958; Krumins *et al.*, 2008) in the presence or absence of 560 ppmv ethene was not distinguishable via quantitative PCR of 16S rRNA genes; possibly this assay was not sensitive enough to detect any small differences in cell numbers (Son, 2009). *Sphingomonas aerolata* (Busse *et al.*, 2003) aerosolized into the same system had a higher 16S rRNA content in the presence of two NMVOC substrates, either ethanol (20 ppmv starting concentration) or acetic acid (240 ppbv starting concentration), than when no substrate was added (Krumins *et al.*, 2014). These results suggested that metabolic activity and biosynthesis in living cells in the air were enhanced in the presence of the volatile substrate. Although the gas phase concentrations of ethanol (20 ppmv), and acetic acid (240 ppbv) used in the laboratory experiments were substantially higher than those reported in the atmospheric environment (Table 5.1), considering the compounds' Henry's law constants, these would produce a maximum of 4 mM in the aqueous phase. Acetic acid and ethanol may both inhibit bacterial growth at high concentrations. Inhibition was observed for many bacteria at 0.5% (weight/weight) (83 mM) acetic acid (Trček *et al.*, 2015). Ethanol was shown to be inhibitory to growth of *E. coli* at 6% vol/vol (1M) (Ingram, 1989). At the other end of the concentration range, the S_{min} for acetic acid was measured at 26 ±12 μM for a *Pseudomonas* strain (Tros *et al.*, 1996), and it has been observed that bacteria can metabolize and grow on combinations of VOCs at low concentrations (Geller, 1983; Shennan, 2006).

Sugars

Of the non-volatile carbon and energy sources in the atmosphere, sugars can be considered readily biodegradable substrates for bacteria. Mono- and di-saccharide (sugar) sources to the atmosphere have been identified as soil and associated microbiota (Simoneit *et al.*, 2004), terrestrial biomass (plant detritus and airborne microbes) (Medeiros *et al.*, 2006), vegetation and plant materials (Samaké *et al.*, 2019b), fungi (Elbert *et al.*, 2007), and marine aerosols (Barbaro *et al.*, 2015; Zeppenfeld *et al.*, 2021). Biomass burning is another source of various sugars to the atmosphere, in particular the stable and widely used tracer, levoglucosan (Fraser and Lakshmanan, 2000; Scaramboni *et al.*, 2015; Simoneit *et al.*, 1999; Urban *et al.*, 2014). Sugars are non-volatile and are associated with aerosol particles of various sizes, constituting dissolved organic carbon in the aqueous phase aerosol (Scaramboni *et al.*, 2015). Antarctic marine aerosols, compared to bulk seawater, showed different relative amounts of monosaccharides (Zeppenfeld *et al.*, 2021), and the authors presented a compelling case that a cause of the observed differences is the bacterial modification of carbohydrates on such aerosol particles.

A series of experiments in the 1970s used laboratory-generated bacterial aerosols of *Serratia marcescens* to investigate the activity and growth of bacteria in air as a test case for potential microbial growth in the Jovian atmosphere. *S. marcescens* in culture medium without a carbon source, but containing nutrients (e.g., ammonia) were aerosolized and introduced into rotating drums simultaneously with water droplets containing the soluble carbon and energy source glucose. $^{14}CO_2$ was produced from ^{14}C-glucose, demonstrating glucose metabolism (Dimmick *et al.*, 1975). Controls indicated that the mineralization of glucose occurred early in the aerial incubation with lesser contributions by microbes that had impacted the walls of the drum after impaction. *S. marcescens* was also shown to incorporate small amounts of ^{3}H-thymidine into biomass (Straat *et al.*, 1977), suggesting DNA formation. Replication of *S. marcescens* in the airborne state in the presence of glycerol and tryptone as carbon and nutrient sources was also observed when compared to loss of particles through settling (Dimmick *et al.*, 1979a; Dimmick *et al.*, 1979b). Interestingly, Dimmick *et al.* (1979a) noted that for continual airborne propagation, aerial bacteria would ultimately need to secure substrates and nutrients from the vapor phase of the atmosphere. Thus, sugars offer potential and readily biodegradable substrates for bacterial survival and even propagation in the air.

Nutrients

Nitrogen

Microbial activity and growth in the atmosphere could be enhanced by the presence of critical nutrients, including nitrogen (N). Microbes may assimilate amino acids, N_2, NH_3/NH_4^+, and NO_3^- as N sources, however, there is a greater energetic cost to the microbe when using oxidized species (Geisseler *et al.*, 2010). Nitrogen species in the atmosphere have been extensively reviewed (Cape *et al.*, 2011). Volatile oxidized nitrogen species in the atmosphere include NOx, made up primarily of nitric oxide (NO) and nitrogen dioxide (NO_2), and nitrous oxide (N_2O). NOx is emitted to the atmosphere at a rate of 38.2 Tg N/yr from combustion processes and other sources, e.g., biogenic sources in soils (Delmas *et al.*, 1997). NOx is short-lived in the atmosphere and is part of the ozone cycle (Nguyen *et al.*, 2022). NO_2 concentrations varied from 10 to 60.7 ppb in urban areas –for a review see Mavroidis and Ilia (2012). N_2O is emitted to the atmosphere at a rate of 17 to 18.5 Tg N/yr through a variety of sources, including agriculture, fossil fuels, industrial sources, waste and wastewater treatment, and biomass burning, and is present in the atmosphere at 336 ppb (Tian *et al.*, 2023).

N_2 constitutes 78% of air and can be assimilated for biosynthesis by nitrogen-fixing bacteria (Kuypers *et al.*, 2018). Reduced N, at the same oxidation state as N in cells, could be supplied to airborne microbes by ammonia (NH_3). NH_3 is a volatile, alkaline gas estimated to be emitted to the atmosphere at 75 Tg NH_3 (expressed as nitrogen) per year (Schlesinger and Hartley, 1992). In air, ammonia levels have been reported to range from <1 ppb to >24 ppb, with a high of 66.9 μg/m^3 related to fertilization periods in agricultural settings (Gu *et al.*, 2022) (Table 5.1). Ammonia is produced from nitrogen cycle processes in soils and the oceans, biomass decay, and burning, and agricultural operations (fertilizers and livestock wastes), with smaller amounts from fossil fuel combustion (Behera *et al.*, 2013). Strain-specific sensitivity to primarily free NH_3 is exhibited differentially by bacteria (Leejeerajumnean *et al.*, 2000) and notably

in anaerobic digesters (Astals *et al.*, 2018; Lay *et al.*, 1998). Inhibitory levels are highly dependent on total ammonia nitrogen, i.e., the total of non-ionized ammonia (NH_3) and ionized ammonium (NH_4^+), and pH (Astals *et al.*, 2018), with higher pH (>8) values presenting the most challenging environments.

Investigations of microbes in the air have revealed evidence for biological processing of nitrogen. Microbiomes of $PM_{2.5}$ collected during Asian dust events ($PM_{2.5} > 36\,\mu g/m^3$) in Korea were compared to those collected on non-events days ($PM_{2.5} < 36\,\mu g/m^3$). DNA encoding functional genes involved in various aspects of the nitrogen cycle were present under both conditions, however on non-event days, 51% of total bacteria 16S rRNA gene sequences were related to nitrogen-fixing bacteria, including *Bradyrhizobium* spp., and the presence of functional genes related to nitrogen fixation increased relative to others (Abd Aziz *et al.*, 2018). While nitrogen fixation activity was not directly assessed, the analysis shows the potential of different air masses to harbor different specific activities. Another intriguing study used Aerosol Time-of-Flight Mass Spectrometry to analyze airborne particles in a Saharan dust plume, which traveled to the North Atlantic region during transport through the atmosphere and found that primary biogenic aerosol particles became enriched in organic nitrogen during transit, while Saharan dust particles did not (Dall'osto *et al.*, 2020). The authors speculated that active microbes associated with the biogenic particles may have carried out nitrogen fixation and assimilation leading to the observed enrichment during transport. Finally, a study of aerosol particles in Hangzhou, China, used metagenomic sequencing to investigate functional genes related to S and N biotransformation (Liu *et al.*, 2020). Genes encoding for ammonification were prevalent, while genes encoding for ammonia oxidation were scarce, suggesting that the accumulation of ammonium could occur. Genes encoding for thiosulfate and sulfite oxidation were present at higher levels than any genes involved in reductive pathways, suggesting sulfate could be produced. Thus, the authors speculated that $(NH_4)2SO_4$ formation as a secondary aerosol could be enhanced through microbial activity –again no direct measures of activity were made (Liu *et al.*, 2020). Although no laboratory studies of aerial microbial activity specifically introduced ammonia with the goal of assessing microbial activity, remnants of media were likely present for numerous studies that ensured cells were not nutrient limited. Intriguing evidence produced from studies with 15N uptake measured via NanoSIMS showed that methanotrophic bacteria growing on filters exposed only to atmospheric concentrations of methane could secure N for biosynthesis through fixation of N_2 or possibly by assimilation of reactive N species (e.g., gaseous ammonia) (Schmider *et al.*, 2024). Clearly, there is a need to gain a better understanding of atmospheric N processing by bioaerosols outside of water droplets.

Phosphorus

Phosphorus, another critical nutrient for microorganisms is primarily associated with aerosols either as solid or soluble forms (Diao *et al.*, 2023; Mahowald *et al.*, 2008), with only phosphine found as a gas (Morton and Edwards, 2005). Total P is present in the atmosphere at about one order of magnitude lower concentration than ammonia (Table 5.1). To our knowledge, there are no studies that have specifically examined P availability to microbes in ambient air outside water droplets, although P sources may have been present in remnants of culture medium in experimental laboratory studies.

⏩ Chemical stressors

pH

pH level is a dynamic property of aerosols in the atmosphere and has a profound impact on biological aerosols. Generally, the survival of microbes decreases with more acidic (i.e., lower) pH levels, because it may lead to denatured proteins (Dill and Shortle, 1991; Goto *et al.*, 1990). Still, microbes have a wide range of capabilities for tolerating acidic pH levels using diverse mechanisms (Guan and Liu, 2020; Schwarz *et al.*, 2022). However, certain microbes, such as non-enveloped viruses, did not have a significant loss in viability when exposed to pH levels ranging from 4 to 10 in droplets when maintained at the same RH (Lin *et al.*, 2020). Due to the impact of pH on microbial survival, it has been speculated that pH would be one of the major limiting factors for life to exist in the Venusian atmosphere, but there might be ways in which the life cycles of airborne microbes might overcome this limitation (Seager *et al.*, 2021). Regardless, low pH levels have a drastic impact upon bioaerosol viability, but there are limitations to our understanding of this due to experimental limitations.

Studies that have aerosolized microbes into the air have not explicitly measured pH, but pH variations have been speculated to have an impact on the bioaerosol (Lin and Marr, 2020). It has been suggested that the loss of infectivity of SARS-CoV-2 in aerosols could be due to the aerosols becoming alkaline (pH ~11) after exhalation from the host. Experimental studies in the bulk phase that closely mimic the chemical composition of the aerosol phase also suggest this possibility (Oswin *et al.*, 2022). It has been demonstrated that a more acidic atmosphere or increased CO_2 concentrations can stabilize SARS-CoV-2's infectivity by preventing the creation of the alkaline aerosol (Haddrell *et al.*, 2024; Haddrell *et al.*, 2023; Luo *et al.*, 2022). This is only applicable for respiratory aerosols, as nascent sea spray aerosols (and other environmental aerosols) are acidic, with pH values ranging from 1.5-4.7 depending upon particle size (Angle *et al.*, 2021). To the best of our knowledge, there have been no laboratory studies conducted at different, explicitly measured aerosol pH values with bioaerosols (especially those derived from environmental sources), which have examined the physiological impact upon microorganisms. It was only recently found that CO_2 concentrations, which affect pH, could have a large impact on respiratory virus infectivity (Haddrell *et al.*, 2024; Oswin *et al.*, 2022). As discussed in those works, the growth medium of many microorganisms contains bicarbonate as a buffering agent. The resulting gas-particle partitioning of this buffer system in the medium is affected by CO_2 concentrations in the atmospheric chamber/system utilized (Haddrell *et al.*, 2024; Oswin *et al.*, 2022), which would affect the pH of the bioaerosols. Overall, this bicarbonate/CO_2 system, along with other vapors, will affect aerosol pH in an experiment. This aspect of experimental aerobiology is only beginning to be understood. Furthermore, experiments exposing bioaerosols to varying pH values in the air are complicated by difficulties in measuring aerosol pH.

Due to the multi-phasic nature of aerosols, there are very few direct measurements of pH in aerosols (Craig *et al.*, 2018). Aerosol pH is affected by humidity, gas partitioning, efflorescence, deliquescence, mixing, and phase separation (Freedman *et al.*, 2019; Tilgner *et al.*, 2021). Due to this complexity, a combination of indirect thermodynamic models and proxy measurements are used along with some direct measurements that

measure bulk aerosol pH (e.g., multiple particles of disparate sizes) (Pye *et al.*, 2020). In general, anthropogenically impacted urban regions have more acidic particles, while areas with less anthropogenic impacts, including oceans and deserts, have more alkaline particles (Karydis *et al.*, 2021). The average bulk aerosol pH of different areas in Europe (range 2.6-6.7; average 3.9), East Asia (range 2.6-7.4; average 4.7), tropical regions (3.2-7.4), eastern USA (average 3.0), Antarctic (4.5-7.0), and northern extra-tropical oceans and Arctic (2.0-7.0; 5.2) (Karydis *et al.*, 2021) vary due to the local emissions. Besides location, the season also affects the pH. For instance, the average pH of $PM_{2.5}$ was 4.5 in winter, 4.4 in spring, 3.8 in summer, and 4.3 in autumn in Beijing (Ding *et al.*, 2019) (Table 5.1). Thus, spatial and temporal pH values must be considered when designing experiments examining aerosol pH and bioaerosols.

Besides the spatial and temporal dynamics of aerosol pH, individual aerosol particles can have different pH values. Recent advances in aerosol pH measurement with Raman spectroscopy have indicated that single particles collected within size fractions (e.g., PM_{10}) of a Korean air sample had pH values of 3.3-5.7 (Yoo *et al.*, 2024). This pH variability among individual particles is likely a result of the heterogeneous composition of particles (e.g., presence of organics, minerals, etc.), and the aerosol aging process (Yoo *et al.*, 2024). For many atmospheric particles, pH variation is likely due to differing concentrations of SO_4^{2-} and NH_3 (Ding *et al.*, 2019). In addition to interparticle variability, there may even be pH variation within a single aerosol particle. However, this heterogeneous intra-particle pH distribution is not yet fully understood at these fine scales (De La Puente and Laage, 2023; Li *et al.*, 2023; Wei *et al.*, 2018). Because the position of a microorganism(s) within a droplet or particle is generally not known, the microbe might be near the outer edge of the droplet, where it would be exposed to acidic conditions, or the droplet may have formed around the microbe, which might expose it to basic conditions. Thus, the pH of a carrier particle or droplet would influence microbial fate and survival in the atmosphere. How differing pH values combined with other open-air factors/stressors would affect bioaerosol viability and survival remains an open question.

Reactive oxygen species

There are multiple reactive oxygen species (ROS) in the atmosphere that can react with bioaerosols. The main oxidizing species are ozone (O_3), hydroxyl radicals ($OH\bullet$), and hydrogen peroxide (H_2O_2). They react with numerous organic compounds and regenerate one another. In the troposphere, ozone can be created through multiple pathways involving nitrogen oxides, VOCs and other organic compounds, and sunlight, as well as through photolysis in the stratosphere (Gligorovski *et al.*, 2015). Once ozone is generated, it can be broken down by ultraviolet light. The photolysis of ozone yields diatomic oxygen, as well as an excited singlet oxygen atom. This reacts with water to form hydroxyl radicals (Figure 5.1). These hydroxyl radicals can react with organic compounds, including CO, resulting in the formation of the hydroxyl peroxy radical ($HO_2\bullet$). Two hydroxyl peroxy radicals can combine to create hydrogen peroxide and oxygen (Figure 5.1). The hydrogen peroxide can break down and create other hydroxyl radicals and reactive atmospheric compounds (Gligorovski *et al.*, 2015). This gas-phase chemistry is complex and interacts with various components of the system discussed here, as well as other parts that are beyond the scope of this chapter. We discuss the role of these major oxidants in relation to bioaerosols.

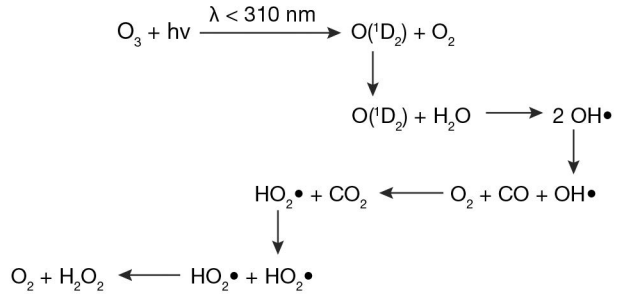

Figure 5.1. Production of main oxidative species in the atmosphere.

Ozone production is not shown, but it is created through various chemical reactions involving nitrogen oxides, volatile organic compounds, and sunlight. UV light breaks down the ozone to create $O(^1D2)$, an excited singlet oxygen atom that reacts with water to create hydroxyl radicals. The hydroxyl radicals can react with biological material and other atmospheric compounds to generate other reactive oxygen species, including H_2O_2. This diagram is based on information presented in Gligorovski *et al.* (2015). © Dillon K. (2025); created in BioRender (https://BioRender.com/cfji7k8).

Ozone

Ozone is a strong oxidant and can kill microorganisms when in high enough concentrations. It readily reacts with various biomolecules, including amino acids (Mudd *et al.*, 1969). Due to its reactivity, ozone is used as an antimicrobial in wastewater treatment (Nasuhoglu *et al.*, 2018), food safety (Dubey *et al.*, 2022), and air disinfection (Liu *et al.*, 2023), although the latter is not advisable for indoor spaces due to potential human exposures and damage to surfaces. At the same time, it is an important component of the stratosphere where it substantially reduces the amount of short-wave UV radiation reaching Earth. However, it is a secondary pollutant in the troposphere and can produce strong negative health effects (Manisalidis *et al.*, 2020). The background concentration of ozone in the clean troposphere is about 20 ppb due to the photostationary reaction. These concentrations can shift to much higher levels due to the reactions between NO_2, radicals, VOCs, and solar energy (Lelieveld and Dentener, 2000; Logan, 1985). Therefore, ground-level concentrations of ozone vary heavily depending on the time of day, season, region, altitude, and local conditions (Hůnová *et al.*, 2023) (Table 5.1). Overall, typical ozone concentrations are 10-100 ppb in the dry troposphere (Wallington *et al.*, 2019) (Table 5.1). In general, ozone concentrations are higher in the summer than in winter, at their lowest levels early in the morning, and reach maximum concentrations in the afternoon when the ozone precursors have had sufficient time to react.

The effectiveness of microorganism inactivation by ozone (i.e., ozone decontamination) is a function of the concentration, exposure duration, and environmental conditions (Liu *et al.*, 2023). For instance, 150 ppb O_3 resulted in the ozonolysis-hydrolysis of an aerosolized octapeptide (Pan *et al.*, 2014). Proteins exposed to 50 and 200 ppb O_3 were found to oligomerize (Table 5.2). As a result, the proteins on the surface of bioaerosol molecules would be modified, which could affect allergenicity and protein function (Liu *et al.*, 2017). Even at low concentrations of ozone (<5 ppb), tryptophan residues of peptides can be oxidized (Pan *et al.*, 2014). Furthermore, the reactions between ozone and peptides are enhanced at higher humidity levels (Pan *et al.*, 2014) which could impact the allergenicity of particles and the physiology of airborne microbes.

Most experiments with ozone have focused on ozone concentrations >100 ppb (Table 5.2). Previous work indicated that 0.06 ppm and 0.2 ppm O_3 can have a large negative impact on microbial viability (Truyols-Vives *et al.*, 2024). At 0.2 ppm, there was a 59.3% and 100% reduction of viability of bacteria and fungi, respectively. When the concentration was 0.06 ppm O_3, there was a ~35% and ~75% reduction in the viability of airborne bacteria and fungi, respectively, in a room (Table 5.2). Concentrations of 60 ppb, or lower, are common in late spring and summer (Table 5.1), so it could be expected that bioaerosol viability is affected. Even though any concentration of ozone may affect microbes, more work needs to be done investigating the effect of lower ozone concentrations on bioaerosols. Lower persistent ozone exposure may affect airborne microbial populations in ways not yet known.

Hydroxyl (OH) radical

Besides ozone, other ROS are prominent in the atmosphere, including OH radicals, which are considered to be the "detergent of the atmosphere" (Gligorovski *et al.*, 2015). The concentration of OH radicals varies throughout the course of the day, but OH radicals are at their highest concentration during the daytime, particularly around midday. In general, the OH concentration in the air can vary from ~10^6-10^7 molecules/cm^3 (~0.1-1 pptv) (Table 5.1) and is affected by environmental conditions (e.g., UV light, VOCs). Due to their ubiquity and abundance, OH radicals interact with many of the biological molecules in the atmosphere. In general, radicals adsorb onto the surface of a bioaerosol and then oxidize cellular components (Estillore *et al.*, 2016), including proteins (Berlett and Stadtman, 1997) and phospholipids (Dilbeck and Finlayson-Pitts, 2013). The oxidation of these compounds could result in the inactivation of microbes; thus, it is a stressor for bioaerosols. Much of the work relating to exposing bioaerosols to hydroxyl radicals relates to air disinfection techniques.

The effect of any one chemical, especially OH radicals, on airborne microorganisms, including their inactivation/death is difficult to attribute because of their complex nature and reactivity with other molecules. Their reactivity also limits their generation and measurement in laboratories. For instance, ozone may be generated as a byproduct, along with various ROS, during OH radical production (Jangra *et al.*, 2023; Prehn *et al.*, 2020). Hydroxyl radicals can be produced as a byproduct of atmospheric reactions with other primary atmospheric disinfectant gases, such as ozone or hydrogen peroxide aerosolized indoors (Truyols-Vives *et al.*, 2024). A decay of triethylene glycol aerosol, another antimicrobial agent for indoor spaces (Desai *et al.*, 2023), can lead to the formation of hydroxyl functional groups and hydroxyl radicals, before ending with the formation of CO_2 and water (Truyols-Vives *et al.*, 2024). Due to the continuous production and destruction of ROS (Chapman, 1930; Truyols-Vives *et al.*, 2024) in such reactions, it is challenging to isolate a specific radical responsible for bioaerosol inactivation (Kinahan *et al.*, 2019). However, certain stressors may be more important than others under specific conditions. For example, OH radicals have been speculated to be the main agent responsible for direct plasma treatments for bioaerosol disinfection (Vaze *et al.*, 2010). It is thought that OH radicals, along with other ROS, are essential components in regulating bioaerosol viability and culturability. When *E. coli* K12 Δ*sodA* (a strain lacking a gene for superoxide dismutase) was levitated in droplets with antioxidants for 20 minutes, there were significant increases in viability

compared to when no antioxidants were added (Oswin *et al.*, 2023) (Table 5.1). Still, more work needs to be done investigating the effect of OH radicals on airborne cells under laboratory conditions that are reflective of the concentrations that are observed in the environment.

Hydrogen peroxide (H_2O_2)

H_2O_2 is another ROS that can have a large impact on airborne microbial survival, as it has been demonstrated to be a disinfectant in indoor environments (Xuan *et al.*, 2020). Hydrogen peroxide oxidizes the molecules present on the surface of microbes. This can generate other radicals, leading to changes of metabolic status of cells or even their death. To combat this stress, cells use enzymes, including catalase to detoxify H_2O_2 and prevent damage (Berlett and Stadtman, 1997). However, this defense is effective only to a degree. For example, when indoor air was treated with 0.5 ppm H_2O_2, there was a ~25% and ~50% reduction in the viability of airborne bacteria and fungi, respectively. At 1 ppm, 100% of fungi and 79.6% of bacteria were inactivated (Truyols-Vives *et al.*, 2024). In hospitals, hydrogen peroxide vapor (up to 120 ppm) or aerosolized hydrogen peroxide (up to ~30 ppm) can be used to disinfect unoccupied rooms (Fu *et al.*, 2012). In another study, 1209 ppm of H_2O_2 slightly reduced the infectivity of bacteriophage MS2, but its efficacy was much lower in killing MS2 and other airborne viruses as compared to other disinfectants (Turgeon *et al.*, 2016) (Table 5.2). While hydrogen peroxide can inactivate microorganisms at high concentrations, such conditions are not representative of what is typically found in the atmosphere.

In general, atmospheric concentrations of H_2O_2 are typically not more than a few ppbv (Table 5.1), which is much lower than what laboratory studies have utilized (Table 5.2). H_2O_2 concentration has a clear seasonal and diurnal pattern, just like ozone: low concentrations in the morning and a peak in the afternoon (Ye *et al.*, 2021). In more polluted areas, such as the North China Plain, the concentration of H_2O_2 can reach 11.3 ppbv during the summer (Wang *et al.*, 2016) (Table 5.1). As discussed previously, the photolysis of H_2O_2 can lead to the production of ROS. In turn, these products could affect other chemical interactions or react with biological molecules (Estillore *et al.*, 2016; Gligorovski *et al.*, 2015; Truyols-Vives *et al.*, 2024). There is a knowledge gap in understanding how a low, persistent exposure to H_2O_2 as is found in the atmosphere affects bioaerosols, along with combinations of other open-air factors.

Metals

Aerosol particles can contain various metal species, including Fe, Al, Mn, V, Zn, Cu, Pb, and others, depending on the particle sources. Cu, Zn, and Fe are especially important for microbes (Zhang *et al.*, 2024). These elements can be found in the atmosphere at concentrations ranging from ng/m^3 to μg/m^3 depending on the location (Table 5.1). For microbes, various metals and heavy metals are required for metabolism (e.g., functioning as enzymatic cofactors) but concentrations that are too high within aerosols can lead to death (Nies, 1999).

Metals mentioned above could be derived from anthropogenic and natural sources (Morales *et al.*, 1996). For example, industrial parks with strong metals emissions, including vanadium smelting activity (Wang *et al.*, 2020), form a hotspot and could

have an additional impact on bioaerosols. In a copper mine, many of the fungal aerosols detected were derived from fungal phylotypes associated with stress tolerance. However, there was no connection between the fungi and a specific source/factor affecting the fungal population's assembly (Fuentes-Alburquenque *et al.*, 2024). In coal mines, it has been suggested that fungal aerosols are significantly impacted by air quality (Cheluszka *et al.*, 2023). Interestingly, the concentrations of bacteria, especially that of *Actinomycetes*, increased as sampling sites approached coal faces (Cheluszka *et al.*, 2023). More information regarding microbial ecology and air quality in mines is needed. Regardless, these emitted metals, whether associated with bacteria or not, could also affect the concentration of ROS in the atmosphere (Mao *et al.*, 2013). It has been found that ROS (Oswin *et al.*, 2023) and other pollutants, as well as metals, shape airborne microbial populations (Zhang *et al.*, 2024).

In the discipline of experimental aerobiology, to the best of our knowledge, there have been no explicit studies that have investigated the effect of metals on bioaerosol physiology. Typically, the aerosolization fluid that is utilized may contain residual metals from growth media or metals that are sorbed to the surface of a cell (Churchill *et al.*, 1995) and/or present intracellularly (Chandrangsu *et al.*, 2017). It is unknown exactly how metals would impact the physiology of these airborne microorganisms, especially given the diversity of metals present in atmospheric particles. In subsurface environments, exposure to multiple metals alters microbial physiology as compared to when a microbe is exposed to a single metal species (Goff *et al.*, 2023). The combination of multiple metals, and other stressors/open-air factors may affect bioaerosol physiology in ways that have not been explored.

Salts

The concentrations of salts in aerosol particles vary depending on the particle source and environmental conditions. Although there are a variety of salts in the atmosphere, sea spray aerosol is a major source, and Na ions are prominent (Lewis and Schwartz, 2004). In some cases, microorganisms themselves could be a source of Na ions, as has been found with fungal bioaerosols in the central Amazon basin (China *et al.*, 2018). Na concentrations can range from >0.1 μg/m^3 in rural terrestrial areas to >1 μg/m^3 in coastal areas (Table 5.1). Na ions can have significant impact upon microbial physiology. Within the context of the atmosphere, the water and Na content in the aerosol particle will have an impact upon the osmotic environment to which the microbe is exposed. As discussed in another section, relative humidity (RH) will have a large impact upon the osmotic conditions of a bioaerosol. Since RH can fluctuate considerably in the atmosphere, the efflorescence and deliquescence points of the salts within aerosols (e.g., relative humidities at which these phenomena occur) will affect the phase states of the aerosol (e.g., solid, semisolid, or liquid), especially when combined with organic compounds including proteins (Huynh *et al.*, 2022; Oswin *et al.*, 2024; Vejerano and Marr, 2018). When an aerosol particle is in the semisolid phase, it is hypothesized that microbes are protected from external stressors (Huynh *et al.*, 2022; Lin *et al.*, 2020). However, the presence of salts will have a large impact upon the physiology of the cells (Dunklin and Puck, 1948). When hypertonic conditions are present in a bioaerosol, then a microorganism will lose water, thus affecting cell functioning. It was found that when the aerosolization fluid

contained 0.5% NaCl, there was an increase in death rates of pneumococci aerosols at intermediate RHs, when compared to distilled water alone as the aerosolization fluid (Dunklin and Puck, 1948). When *P. syringae* R10.79 cells were aerosolized from a 35 g/L NaCl solution, they had increased hygroscopicity as compared to when aerosolized from pure water (Nielsen *et al.*, 2024). Although the exact salt concentrations in the individual aerosols were not measured, it can be expected that the airborne bacteria generated with high NaCl concentrations experienced hypertonic conditions. However, not many studies have been conducted due to the complicated multi-phase considerations of these studies. Other studies used stationary droplets as a surrogate for aerosols to examine the effect of different osmotic conditions to microbes on surfaces (Alsved *et al.*, 2018; Lin and Marr, 2020; Lin *et al.*, 2020). It was suggested that osmoregulation could be improved when *P. syringae* R10.79 cells in stationary droplets are dried in the presence of sea salt, i.e., there was improved culturability as compared to drying when only pure NaCl was present (Alsved *et al.*, 2018). Specific microorganisms, including *Thiobacillus*, were found to be correlated with the presence of certain salt cations in $PM_{2.5}$ (Hong *et al.*, 2024). It is possible that these salt cations help to promote the survival of these bacteria.

Regardless, in the multi-phase atmosphere, it has been suggested that low quantities of water (i.e., hypertonic conditions), is likely not a major driver of viability loss of airborne *E. coli* (Oswin *et al.*, 2023). However, airborne *Streptococcus pyogenes* survival was controlled by the composition of an airborne droplet (including salt concentrations). It was observed that at low humidities, the efflorescence of aerosol particles drove viability loss of *S. pyogenes*. Finally, it should be noted, that the tolerance of an airborne cell to these circumstances can be affected by its physiological state (i.e., stage in culture growth prior to aerosolization) (Otero-Fernandez *et al.*, 2024). The preparation of the microbial material always needs to be considered when conducting experimental aerobiology experiments, as it may impact the results (Alsved *et al.*, 2020).

⏩ Physical stressors

Temperature and humidity

Temperature and humidity are some of the most studied parameters affecting airborne microorganisms and their survival (Tang, 2009). While temperature and humidity can act as individual stressors, in most cases, we must consider their interaction, which is complex and often species-specific. Other environmental factors also play a role. In general, it was observed that microorganisms exhibit the highest survival rates at very low (<25%) and very high humidity levels (>80%) (Cox and Goldberg, 1972; Wright *et al.*, 1969). However, this relationship is not universal, and as early as 1935, Wells showed that *E. coli* was inactivated at a higher rate when humidity approached saturation levels (Wells, 1935).

The amount of moisture in the atmosphere could be expressed in absolute terms, such as absolute humidity (amount of moisture in the air), or relative humidity (RH, percent of the maximum amount of water vapor that the air could hold at a given temperature). One can also consider water activity (typically denoted as a_w), which is water availability in a substance, such as a surface, to which microorganisms

are attached. Thus, the ability of microorganisms to survive in the air as a solitary organism or when attached to a surface will depend on the amount of moisture available to it from the air or surface. However, as mentioned, microorganism survival as a function of RH is not linear and depends on microorganism type (e.g., virus, bacteria, or fungus) and species.

Most of us are familiar with the temperature and humidity levels we encounter at the ground-level troposphere: from relatively low moisture content in winter (e.g., ~5 g/m^3 of vapor at 0°C and 100% RH) to much higher moisture content in summer (e.g., 14 g/m^3 of water vapor at 30°C at 50% RH) and temperatures typically varying from subzero °C in winter and up 30°C or so in summer. At stratospheric altitudes (12-50 km), the temperature and humidity levels are drastically lower (Dassarma and Dassarma, 2018) and survival of microorganisms under such conditions presents a challenge. Even at tropospheric altitudes, microorganism survival outside of droplets is a challenge due to low temperature and limited moisture that typically decrease with height, with temperatures ranging from –60°C to 15°C (Vargin *et al.*, 2015) (Table 5.1).

However, relatively few direct measurements examined the effect of temperature and humidity on the survival of microorganisms in the stratosphere or troposphere outside of clouds. Most of our knowledge comes from chamber, near-ground measurements, or via the examination of temperature and RH effect on the transmission of infectious organisms. This brief overview looks at the effects of humidity and temperature on the survival of viruses, bacteria, and fungi.

Viruses

While some studies argue that absolute humidity, rather than relative humidity, modulates the survival of viruses, such as influenza (Mcdevitt *et al.*, 2010), the combination of temperature and RH provides a better and mechanistically sound explanation of the observations (Marr *et al.*, 2019).

In general, enveloped viruses like influenza and coronaviruses tend to survive better at lower humidity levels, while non-enveloped viruses, like adenoviruses, tend to stay more stable at higher RH (Sobsey and Meschke, 2003; Tang, 2009; Yang and Marr, 2012). U-shaped survival of both airborne MS2 (non-enveloped bacteriophage) and Φ6 (enveloped bacteriophage) was also reported (Lin and Marr, 2020) (Table 5.2). Yang and Marr (2012), as well as other sources (Guo *et al.*, 2021), provided an extensive compilation of studies describing the survival of viruses at various RH levels. At RH below 40%, viral particles can remain airborne longer and retain infectivity (Marr *et al.*, 2019; Tang, 2009). Midrange humidity around 40-60% RH is often less favorable for viral survival (Casanova *et al.*, 2010; Guo *et al.*, 2021). Very high humidity (>80% RH) may also allow some viruses to survive well (Tang, 2009). Experiments with the SARS-CoV-2 Delta variant showed better survival and higher infectivity at 90% than at 40% RH, however, there was infectivity loss in both cases, but, as proposed, due to different mechanisms (Haddrell *et al.*, 2023) (Table 5.2). This V or U-shaped survival appears to apply to both surface-bound and aerosolized viruses.

Table 5.2. Laboratory studies of effect of chemical and physical stressors and growth enhancers on microorganisms aloft.

Parameter	Concentration	Lab Apparatus	Bioaerosol	Reference
Growth substrates and nutrients				
Methane	1,500 ppmv	Rotating drum	Methanotrophic enrichment cultures	Dillon *et al.*, 2022
Ethene	560 ppmv	Rotating drum	*Xanthobacter autotrophicus*	Krumins *et al.*, 2008; Son, 2009
Ethanol	20 ppmv	Rotating drum	*Sphingomonas aerolata*	Krumins *et al.*, 2014
Acetic acid	240 ppbv	Rotating drum	*Sphingomonas aerolata*	Krumins *et al.*, 2014
Glucose (aqueous)	0.5%, 5 g/L 100 μCi/mL	Rotating drum	*Serratia marcescens*	Dimmick *et al.*, 1975
Chemical factors				
Ozone	0.001 – 0.071 ppm	Chamber	*Staphylococcus xylosus* DSM 20266	Clauß *et al.*, 2022
	0 and 150 ppb	Rotating drum	Octapeptide	Pan *et al.*, 2014
	>300 ppb	Rotating drum	*Yersinia rohdei* and MS2 phage	Santarpia *et al.*, 2012
	0 and 150 ppb	Rotating drum	*Bacillus thuringiensis* Al Hakam spores and MS2 phage	Ratnesar-Shumate *et al.*, 2015
	100 ppb	Rotating drum	*E. coli*	Kinahan *et al.*, 2019
	100 ppm	OT-RS system	*Broussonetia papryifera* pollen fragment	Gong *et al.*, 2019
	200, 400, 800, 1200 ppm	OT-RS system	*Aspergillus fumigatus*, *Aspergillus versicolor*, *Cladosporium, herbarium*, *Paecilomyces variotti*, *Penicillium camembertii*, *Penicillium chrysogenum*, *Penicillium digitatum*	Ai *et al.*, 2022
	0.1, 1.1, 3.3 ppm	Chamber	*E. coli* var communis, *Micrococcus albus*	Dark and Nash, 1970
	0.05, 0.1, 2 ppm	Chamber	*Micrococcus luteus*	Bailey *et al.*, 2007
H_2O_2	0.5, 1 ppm	Room	Indoor microbiome (bacteria and fungi)	Truyols-Vives *et al.*, 2024
	1209 ppm	Chamber	MS2, ϕ6, ϕX174	Turgeon *et al.*, 2016

Parameter	Concentration	Lab Apparatus	Bioaerosol	Reference
Salt (Na^+)	0.5% NaCl in aerosolization fluid	Chamber	Pneumococcus type I	Dunklin and Puck, 1948
	35 g/L NaCl aerosolization fluid	Flow tube	*Pseudomonas syringae* R10.79	Nielsen *et al.*, 2024
			Physical factors	
Temperature and RH	6 days at 33% RH	Containers	*P. syringae* pv. *garcae* 158, *P. syringae* pv. *syringae* 281, E. coli LB, E. coli L_{NP}	De Araujo *et al.*, 2019
	6 days at <5% RH	Containers	*P. syringae* pv. *garcae* 158, *P. syringae* pv. *syringae* 281, E. coli LB, E. coli L_{NP}	De Araujo *et al.*, 2019
	10, 35, and 90% at 23°C.	Rotating drum	Newcastle disease virus, infectious bovine rhinotracheitis virus, vesicular stomatitis virus, and *Escherichia coli* B T3 bacteriophage	Songer, 1967
	Bacteria: 1 h at 20, 40, 60, 80, and 100% RH Viruses: 1 h at 23, 33, 43, 55, 75, 85, and 100% RH	Rotating drum	*Escherichia coli, Mycobacterium smegmatis, MS2, Φ6*	Lin and Marr, 2020
	From −40 to 49°C	Chamber	*Serratia marcescens*, *Escherichia coli*, and *Bacillus subtilis* var. *niger* spores	Ehrlich *et al.*, 1970
	Three temperatures (7.0–8.0°C, 20.5–24.0°C, and 32.0°C) and five RHs (20–25%, 34–36%, 49–51%, 64–65%, and 81–82%).	Rotating drum	Vaccinia, influenza, Venezuelan equine encephalomyelitis, and poliomyelitis	Harper, 1961
	Temperatures of 4°C, 20°C, and 40°C. At each temperature, RH of 20% ± 3%, 50% ± 3%, and 80% ± 3%	Sealed chamber and stainless-steel coupons	Gastroenteritis virus (TGEV) and mouse hepatitis virus (MHV)	Casanova *et al.*, 2010
	19°C and 25°C at 75% RH	Rotating drum	*Φ6*	Prussin *et al.*, 2018

Table 5.2. (continued)

Parameter	Concentration	Lab Apparatus	Bioaerosol	Reference
Temperature and RH	18, 25 and 35°C with three humidity levels (35%, 65%, and 95% RH) per temperature	Release of bacteria from infected cucumber leaves in an aerosol chamber	*Pseudomonas amygdali pv. lachrymans*	Chai *et al.*, 2023
	Pressures as low as 2 kPa and temperatures as low as –50°C, with varying sun angle; $6.25{\cdot}10^3$ and 68.8 $mJ{\cdot}cm^{-2}$ of UV-A and UV-B radiation, respectively	Stratospheric balloon flight experiment	*Bacillus subtilis* endospores	Heitkämper *et al.*, 2024
	UV fluence of 6 mW/cm^2, Temperature from 21°C to –51°C	Stratospheric balloon flight experiment	*Aspergillus niger* spores, *Staphylococcus capitis* subsp. *Capitis, Alinisphaera shabanensis and Buttiauxella p. MASE-IM-9*	Cortesão *et al.*, 2021
UVA	54.54 W/m^2 × 6 hours	Chamber to simulate the stratosphere; coupons with bacteria	Stratosphere-isolated and ground-isolated *B. subtilis* spores; 99.9% inactivation	Smith *et al.*, 2011
UVB	5.11 W/m^2 × 6 hours	Chamber to simulate stratosphere; coupons with bacteria	Stratosphere-isolated and ground-isolated *B. subtilis* spores; 99.9% inactivation	Smith *et al.*, 2011
UVC	0.00421 W/m^2	Chamber to simulate the stratosphere; coupons with bacteria	Stratosphere-isolated and ground-isolated *B. subtilis* spores; 99.9% inactivation	Smith *et al.*, 2011
UVA + UVB	19.4 W/m^2 + 0.6 W/m^2	Chamber	Cells and spores of *Bacillus* from Kosa and *B. subtilis* from soil; up to 35 hours	Kobayashi *et al.*, 2015

Parameter	Concentration	Lab Apparatus	Bioaerosol	Reference
UVC	70.3, 73.3, and 18.3 J/m^{-2}	Chamber	*B. atrophaeus*, *P. agglomerans*, and *Y. ruckeri*; 90% inactivation; 170-330 seconds	King *et al.*, 2011
UVC	8.3–197 J/m^{-2}	Chamber, Air and surface exposures	Various viruses, bacteria, and fungal spores	Brickner *et al.* (2003) and references therein
UVGI (UVC)	339–423 μW sec/cm^2 for single-stranded RNA and 910–1,196 μW sec/cm^2 for double-stranded DNA	Chamber	Single and double-stranded RNA and DNA viruses; 90% inactivation	Tseng and Li, 2005
UVGI (UVC)	809–909 μW sec/cm^2 for single-stranded RNA and 1,906–2,005 μW sec/cm^2 for double-stranded DNA	Chamber	Single and double-stranded RNA and DNA viruses; 99% inactivation	Tseng and Li, 2005
UVC	3–140 J/m^2		Single-stranded RNA and double-stranded DNA viruses	Lytle and Sagripanti (2005) and references therein
UVC	2,608 μW sec/cm^2 (26 W/m^2)	Chamber	Adenovirus and MS2	Walker and Ko, 2007
UVC	599 μW sec/cm^2 (6 W/m^2)	Chamber	Murine Hepatitis Virus Coronavirus	Walker and Ko, 2007
UVA + UVB	From 45/29 to 272/175 kJ/m^2	Chamber	*P. syringae* pv. *garcae* 158, *P. syringae* pv. *syringae* 281, *E. coli*, up to 60 min	De Araujo *et al.*, 2019
UVC	57–829 μW sec/cm^2	Chamber	*Serratia marcescens* and *Mycobacterium bovis BCG*	Ko *et al.*, 2000
UVC	Average spherical irradiance of 7.53 μW/cm^2	Chamber	*S. marcescens*, *B. subtilis*, and *M. parafortuitum*	Peccia *et al.*, 2001
UVC	200–14,000 μW/cm^2	Chamber	*Escherichia coli, Bacillus subtilis spores,* cells of *Candida famata var. flareri,* and spores of *Penicillium citrinum.*	Lin and Li, 2002

Table 5.2. (continued)

Parameter	Concentration	Lab Apparatus	Bioaerosol	Reference
Electrostatic Charge	From 4,100 negative to >2,700 positive charges	Aerosol chamber	*Pseudomonas fluorescens* and *Bacillus subtilis*	Mainelis *et al.*, 2002
	B. subtilis var niger: 93% with 13–42 negative charge units; 5% positive 42–195 or higher charge. *P. fluorescens:* mostly negative 14–34 units	Aerosol chamber	*B. subtilis* var *niger* and *P. fluorescens*	Xie *et al.*, 2011
Electrostatic field	15 kV for 30 min, 5 and 10 kV for 2 hr for filter exposure; 10 kV for 30 seconds for airborne exposure	Bacteria on filters; bacteria in the air.	*P. fluorescens* and *B. subtilis* var. *niger* cells	Yao *et al.*, 2005
	10 kV/cm	Captured by electrostatic precipitation	Non-enveloped (Ad5) and enveloped (SARS-CoV-2 pseudotyped lentivirus)	Preston *et al.*, 2023
Non-speciated particulate matter	Bacteria captured on filters at different soot concentrations and exposed to UVC for 15, 30, and 60 s.	Chamber	*Mycobacterium smegmatis*	Noda *et al.*, 2022
	Bacteria aerosolized with PBS, Mongolian desert dust, and sludge dust control	Chamber	DH5α *Escherichia coli*	Noda *et al.*, 2019
	Airborne Arizona Road Dust ranging from 250 to 2,000 μg/m^3	Chamber	*E. coli* K12 (JM109) and *E. coli* JM109-pEC958	Agarwal *et al.*, 2024

Survival and infectivity of non-enveloped viruses such as rhinovirus and adenovirus increased slightly when RH was increased from very low levels to around 50%. However, such increased humidification reduced the infectivity of the enveloped flu virus (Aganovic *et al.*, 2022). In an experiment with a rotating drum, Newcastle disease virus and vesicular stomatitis virus (both enveloped) survived best at 10% RH and 23°C. On the other hand, infectious bovine rhinotracheitis virus (enveloped) and *E. coli* B T3 bacteriophage (non-enveloped) survived storage at the same temperature best at 90% RH (Songer, 1967). The infectivity of Φ6 was shown to decrease by two orders of magnitude going from 19 to 25°C at 75% RH (Prussin *et al.*, 2018) (Table 5.2). The negative effect of temperature on the survival of various viruses was also reported in other reviews (Guo *et al.*, 2021). The survival decreased further after prolonged exposures.

Experiments in a rotating drum showed that vaccinia, influenza, Venezuelan equine encephalomyelitis, and poliomyelitis viruses survived better at low temperatures and low relative humidity. Interestingly, poliomyelitis virus survived better in high humidities compared to lower humidities (Harper, 1961).

Other environmental factors, such as carrier particles, modulate the survival of viruses at certain humidities. For example, saliva emitted with viruses like murine hepatitis virus (MHV), which was used as a proxy for SARS-CoV-2, could act as a protective barrier, especially at low humidity levels (Nieto-Caballero *et al.*, 2022). Temperature as a single stressor has been shown to affect the survival of the influenza virus, independent of humidity (Irwin *et al.*, 2011).

Viruses attached to soil, dust, or marine organic aggregates can be transported across the free atmosphere. It was estimated that above the atmospheric boundary layer, the downward flux of viruses ranged from 0.26×10^9 to $>7 \times 10^9$ m^{-2} per day, mostly from marine sources (Reche *et al.,* 2018). These deposition rates were 9-461 times greater than those for bacteria. There is evidence that viruses may remain viable/infectious after atmospheric transport (Prospero *et al.*, 2005; Sharoni *et al.*, 2015).

Bacteria

In general, many bacteria tend to survive better at higher humidity levels above 60% RH (Dunklin and Puck, 1948; Lin and Marr, 2020; Tang, 2009). For example, *M. smegmatis, E. coli,* and *B. subtilis* showed little decay with RH above 60%, but their viability below 60% was lower and varied with species (Lin and Marr, 2020). However, this relationship is not universal, and the effect of humidity on the survival of bacteria depends on species and interaction with other environmental parameters. For example, pneumococci show peak decay rates around 50% RH, with better survival at both lower and higher humidity levels (Dunklin and Puck, 1948), and some bacteria survive better at very low or very high humidity levels (Tang, 2009).

Obviously, temperature also affects the survival of bacteria. A study of survival of airborne *S. marcescens*, *E. coli*, and *B. subtilis* var. *niger* spores at different temperatures (from –40 to 49°C) showed that the decay of *B. subtilis* var. *niger* was not significantly affected by temperature, while the decay rate of the two vegetative microorganisms increased with increasing temperature, but the decay slope was different (Ehrlich *et al.*, 1970) (Table 5.2). However, at the early stages of airborne suspension (4 min), the survival of all three microorganisms showed a plateau between –20 and 20°C, with lower recovery at lower and higher temperatures.

According to another study, a relatively lower temperature of around 25°C and high humidity (95% RH) support prolonged bacterial survival in aerosols; in contrast, higher temperatures (35°C) combined with much lower humidity (35% RH) can have a synergistic effect in accelerating bacterial decay in aerosols (Chai *et al.*, 2023).

The composition of the aerosolized suspension (e.g., salts, proteins) influences bacterial survival at different humidity levels. Type I *Pneumococcus*, aerosolized from broth, saliva, or 0.5% saline showed a very high inactivation rate at RH of ~50%. However, when a saline-free solution was used, the sharp decay peak at mid-range humidities disappeared (Dunklin and Puck, 1948), demonstrating the importance of the surrounding environment and coating material on the survival of bacteria (Table 5.2). The inactivation was even stronger at higher temperatures. The survival of hemolytic *streptococcus* group C and *staphylococcus* exhibited similar patterns.

Thus, bacteria adapted to survive in arid conditions would likely fare better in a stratospheric environment, where humidity levels are low. Two strains of *P. syringae*, pv. *syringae* IBSBF 281T (pathovar type strain) and pv. *garcae* IBSBF 158, were tested at RH 33% and <5%, placed in containers with appropriate desiccants. After 6 days of exposure to <5%, 22% of IBSBF 158 survived, while the viability of the 281 strain was reduced by 3-4 orders of magnitude. However, at 33% RH, only 4% of the 158 strains survived, 10× higher than the 281 strain. For comparison, at both RH levels, the survival of *E. coli* was 3-4% (De Araujo *et al.*, 2019) (Table 5.2).

Deinococcus radiodurans R1 (ATCC 13939), *E. coli* MG1655, and 15 isolates collected from as high as 38 km above sea level during a balloon flight were grown and placed in a desiccation chamber in liquid droplets at 25% RH. Three-quarters of non-sporulating isolates were desiccation tolerant with survival greater than that of *E. coli* (Bryan *et al.*, 2019).

B. subtilis spores exposed to stratospheric conditions (pressures as low as 2 kPa and temperatures as low as −50°C) for 3.5 hours and protected from the sun's UV rays survived sufficiently well to serve as a control for samples exposed to different UV doses (Heitkämper *et al.*, 2024).

Some bacteria seem to be extremely well adapted to low humidity conditions. *Gloeocapsopsis* AAB1, isolated from the Atacama Desert, biosynthesized sucrose and trehalose at water activity (a_w) level as low as 0.4 (Azua-Bustos *et al.*, 2014). Some sources consider water activity of 0.54 a limit for detectable anabolic activity (Paris *et al.*, 2023).

Fungi

Fungi generally favor more humid conditions for survival and growth (Hiwar *et al.*, 2021) and many can grow rapidly at temperatures between 20°C to 30°C, provided they have sufficient nutrients and moisture. However, some exceptions provide a better understanding of life under severe water-limiting conditions, such as those found in the stratosphere (Stevenson *et al.*, 2017; Rangel *et al.*, 2018). For example, *Aspergillus penicillioides* can germinate at a low water activity of 0.585 a_w (approximately 58.5% of relative humidity).

Fungal spores of *Aspergillus niger* aboard a balloon flight to the middle stratosphere (~38 km altitude) were not affected during a 5+ hour flight when deposited both as a monolayer and multilayer when protected from UV. However, their germination was delayed compared to laboratory controls (Cortesão *et al.*, 2021).

UV light

Microorganisms in the atmosphere are constantly bathed by UV rays, which have long been known to have germicidal activity due to DNA and RNA damage (Bono *et al.*, 2021). The UV spectrum is typically divided into four ranges: vacuum ultraviolet (VUV; <200 nm), UVC (200-280 nm), UVB (280-315 nm), and UVA (315-400 nm) (Kesavan and Sagripanti, 2013). VUVs are the most energetic waves and readily interact with oxygen atoms in the stratosphere; their interaction with organic molecules is detrimental even at low doses (Cutler and Zimmerman, 2011). UVC is often referred to as the germicidal spectrum due to its strong ability to inactivate microorganisms. UVB causes "sunburn" and also helps synthesize Vitamin D (Goodsell, 2001). UVA has the longest and least energetic wavelengths of the UV spectrum, yet it constitutes 95% of the total energy of the UV spectrum that reaches the Earth's surface (Dassarma *et al.*, 2020).

The inactivation (or survival) of airborne microorganisms exposed to UV light depends on multiple factors, including UV wavelength, radiation intensity, interaction time, susceptibility of microorganism species, relative humidity, temperature, and the type and nature of carrier particle(s) (e.g., microorganism cluster or non-biological carrier, such as particulate matter).

Role of wavelength and dose

Since VUV and UVC radiation (<280 nm, or far-UV) are readily absorbed by ozone and oxygen in upper atmospheric layers before sunlight reaches the earth, far-UV radiation has limited relevance to the inactivation of airborne microorganisms in the troposphere. However, as discussed in other parts of this chapter, some microorganisms may be found at altitudes as high as 80 km, substantially above the stratospheric ozone layer. Thus, they would be subjected to radiation by UVC or even VUV at those altitudes.

The survival of microorganisms exposed to UV depends on the received dose (fluence, W s /m^2 or J/m^2), which is the product of UV intensity (flux, W/m^2) and exposure time (s). After sufficiently high doses are received, exposed microorganisms are inactivated (Spicer, 2021), although the dose depends on multiple factors, including microorganism species and environmental humidity. Since the primary application of UVC is to disinfect various indoor spaces and surfaces, most information about the fluences needed to inactivate microorganisms comes from theoretical estimates and indoor or chamber studies (Table 5.2). King *et al.* (2011) reported that the fluence of UVC (254 nm) required for killing 90% of *B. atrophaeus*, *P. agglomerans*, and *Y. ruckeri* cells was 70.3 J/m^2, 73.3 J/m^2, and 18.3 J/m^2, respectively. The fluences needed to inactivate the same organisms on the surface were 128 J/m^2, 28.1 J/m^2, and 16.3 J/m^2. Thus, attachment of airborne microorganisms to other particles may offer a degree of protection from lethal UV rays depending on species. In laboratory chamber studies, Peccia *et al.* (2001) reported that fluence between 25 and 32 J/m^2 was needed to inactivate airborne *Serratia marcescens, Bacillus subtilis,* and *Mycobacterium parafortuitum* at 90% RH (Table 5.2).

Even if atmospheric oxygen absorbs UVC and part of UVB, the amount of UVA and UVB reaching the boundary layer is sufficient to inactivate certain airborne microorganisms (Xue and Nicholson, 1996). According to a compilation of data by Madronich *et al.* (2018), UVB is more potent than UVA on an energy basis, but there is a large variability in sensitivity among bacteria.

In general, the UVB radiation is stronger at low latitudes, during summer months, and during solar noon (Kesavan and Sagripanti, 2013). It is also stronger at higher altitudes: the intensity of UVB at 850 m in São Paulo, Brazil, was reported as 9.3 W/m²; at an altitude of 5,091 m at the Atacama Desert, Chile, it was 15.6 W/m² (Pulschen *et al.*, 2015). The ground-level DNA-damaging fluence rates averaged from 1979 to 2000 were found to vary greatly depending on geographical location and season, with values ranging from 40 to 360 J/m^2/day (Madronich *et al.*, 2018) (Table 5.1). Current UVA and UVB intensities are provided by the UVB Monitoring and Research Program (UVMRP) at http://UVB.nrel.colostate.edu.

If the amount of DNA-damaging radiation is used as a normalizing metric, then a summer day radiation of 100 J/m^2 would reduce the viability of *S. typhimurium* by 37% (1 e^{-1} reduction) within 3 minutes (De Araujo *et al.*, 2019). Thus, if damage by UV is considered separately from other stressors, the airborne bacteria would survive longer in winter than in summer, with the shortest survival times in the tropics regardless of the season (Madronich *et al.*, 2018).

Lytle and Sagripanti (2005) tabulated the literature and determined a UV dose needed to reduce viability by 37% (i.e., e^{-1}) based on sensitivity normalized to genome size. The dose predicted to achieve one e-folding varied from single digits to almost 400 J/m^2, depending on virus species. Based on sensitivity data and the 254-nm-effective solar flux (J/m$^2_{254}$/min) ranging from 0.17 (Griffin, GA) to 0.80 (Hilo, Hawaii), 1-log inactivation of the *Filoviridae* family of viruses would be achieved between 100 and 21 minutes. Based on modeling, the infectivity of some viruses would decrease by 3 logs (99.9%) when exposed to a full day of sun (Ben-David and Sagripanti, 2010).

While most of the microorganisms would experience UVA and UVB light at tropospheric altitudes, those that manage to reach the stratosphere would be exposed to UVC as well. Smith *et al.* (2011) simulated stratospheric conditions (-70°C temperature and 56 mb pressure) using both stratosphere-isolated and ground-isolated *B. subtilis* strains. The spores of these bacteria were exposed to 0.00421, 5.11, and 54.64 W/m^2 for six hours of UVC (200-280 nm), UVB (280-315 nm), UVA (315-400 nm), respectively, and 99.9% of spores were killed in all cases (Smith *et al.*, 2011). Similar inactivation of *B. subtilis* spores was achieved during stratospheric balloon flights (Heitkämper *et al.,* 2024) (Table 5.2).

Role of the carrier particles and the surrounding environment

If microorganisms are in a microbial cluster or a cluster of nonbiological particles, it could be expected that the outer layer will offer a protective role for the internal layer against direct radiation and desiccation (Heitkämper *et al.*, 2024). According to calculations by Coohil (1986), 61% of the incident 254 nm light will be transmitted through one organism. If two microorganisms are shielding the third, the amount of transmitted incident light will decrease by more than 60% (Kesavan and Sagripanti, 2013). It was found that 11 out of 12 microorganisms recovered from Saharan dust were able to resist an intense UVC radiation (30 W, ~80 μW /cm^2) for 1 min, while 5 isolates resisted for 5 min, suggesting that at least part of bacterial community carried by dust can withstand challenging conditions during their transport, including radiation (Federici *et al.*, 2018). The UV radiation tolerance of *B. subtilis* spores within Kosa (Asian dust) was higher compared to a soil bacterium and even to soil bacterial spores (Kobayashi *et al.*, 2015) (Table 5.2). Certain components of the carrier particle, such

as soil minerals, offer protection to organic compounds from radiation (Ertem *et al.*, 2021). The atmospheric conditions, such as the presence of clouds, can substantially affect the UV fluence rates above, below, and within the cloud, thus offering spaces with lower UV radiation. Cloud droplets themselves can enhance the fluence rates within droplets due to diffraction (Mayer and Madronich, 2004).

Role of microorganism species

Microorganism survival when exposed to UV is substantially affected by microorganism species (Peccia *et al.*, 2001; Xu *et al.*, 2003), as was already touched upon earlier. An extensive compilation of actinic radiant exposure at 254 nm needed to inhibit colony formation in 90% of certain bacteria, spores, and viruses on agar plates and air is presented by Brickner *et al.* (2003) with a list of predicted sensitivities published elsewhere (Lytle and Sagripanti, 2005). The dose of UVC needed to achieve 90% inactivation varied from 339-423 μW sec/cm^2 for single-stranded RNA viruses, to 910-1196 μW sec/cm^2 for double-stranded DNA viruses (Table 5.2). The dose needed for 99% inactivation was about 2× higher (Tseng and Li, 2005).

The loss of microbial viability due to UV exposure is dictated primarily by the presence or absence of a cell wall and the thickness of the cell wall (Jagger, 1985). The genus *Clostridium*, which has endospore-forming bacteria, has enhanced resistance to atmospheric stressors, including UVB (Smith *et al.*, 2018). The same could be said about endospore formers such as *B. subtilis* (Heitkämper *et al.*, 2024). In addition, pigmented microorganisms are more UV-resistant, as pigments act as shields against UV (Kellogg *et al.*, 2004; Tong and Lighthart, 1997). Airborne non-enveloped viruses like influenza, smallpox, and adenovirus are relatively easily inactivated by UV, but still offer stronger resistance than enveloped viruses, such as coronaviruses. While 30% of adenovirus survived 16.2-second exposure to UVC of 2608 μW s /cm^2, only 12% of coronavirus survived the same 16.2-second exposure to 599 μW s /cm^2 (Walker and Ko, 2007). Fungi like *Cladosporium* species tend to be more UV-resistant (Cutler and Zimmerman, 2011). The conidia of *Aspergillus* were found to be more resistant to UV than the conidia of *Penicillium* or vegetative cells of *Micrococcus* and *Mycobacterium* (Lysenko, 1980). This resistance helps fungi to spread outdoors over extended periods of time and distances.

Some yeasts also exhibit extraordinary resistance to UV. *Naganishia friedmannii* were transported by a stratospheric balloon to over 100 km, and *N. friedmannii* displayed good survival even after UV exposure. On the other hand, exposure of *Holtermanniella watticus* to UV reduced its survival to essentially zero (Pulschen André *et al.*, 2018).

The viability of *Bacillus pumilus* SAFR-032, a radiation-tolerant strain, was reduced by four orders of magnitude after exposure to the atmosphere at 31 km for four hours (Khodadad *et al.*, 2017). A similar inactivation rate was observed in ground tests. Exposure of *Bacillus* sp. strain PS3D and *Deinococcus radiodurans*, which is known for its extraordinary resistance to desiccation and high doses of ionizing radiation, space conditions, and extreme UV radiation (10-100 nm), showed that exposure to UV reduced the viability of those bacteria by about an order of magnitude after their viability had already been reduced by 2-3 orders of magnitude by exposure to space vacuum (pressure 10^{-6} Pa) (Saffary *et al.*, 2002). Still, some cells survived even these extreme exposures, showing their ability to survive composite stress factors.

Role of relative humidity on the effect of UV on microorganisms

Typically, the inactivation of bacteria by UV is less efficient at higher RH (Cutler and Zimmerman, 2011; and references therein), but some bacteria respond with the opposite effect or no effect at all, and viruses respond with mixed effects (Kesavan and Sagripanti, 2013). Low susceptibility of bacteria to UV at high RH and high susceptibility at low RH were noticed as early as 1940 (Whisler, 1940). *E. coli*, *M. parafortuitum*, and *Staphylococcus epidermis* showed low susceptibility during high RH conditions, but inactivation of some strains of *S. marcescens* increased at higher RH levels (Kowalski, 2010). When exposed to UV, *S. marcescens* showed an increased survival at higher RH levels, with resistance increasing dramatically at RH >85% (Ko *et al.*, 2000; Riley and Kaufman, 1972). *S. marcescens*, *B. subtilis*, and *M. parafortuitum* were observed to sorb water at high RH, and that led to lower inactivation (Peccia *et al.*, 2001). Lin and Li (2002) found that three types of bacteria and one type of fungal spores had lower susceptibility to UV at 80% RH than at 50% RH.

The susceptibility of vaccinia virus deposited on stainless steel surfaces increased with decreasing RH (Mcdevitt *et al.*, 2010), but fractional survival of airborne influenza was higher at humidity of 75% compared to 25% and 50% RH (Mcdevitt James *et al.*, 2012). The susceptibility of four viruses to UV increased at 55% RH compared to 85% levels (Tseng and Li, 2005).

Role of temperature on microorganism inactivation by UV

Structural changes of biological molecules, including membrane phospholipids, proteins, and DNA (Kesavan and Sagripanti, 2013), can occur when temperatures are high. UV effectiveness against *S. marcescens* and *Mycobacterium bovis* (BCG) substantially and significantly increased when temperature increased from 4 to 25°C (Ko *et al.*, 2002). When temperatures are high, UV radiation is more likely to cause mutations, as cells are more metabolically active and the DNA is more flexible (Kesavan and Sagripanti, 2013).

Electrostatic charge

Electrical charge plays a significant role in the behavior, viability, motion, and collection of airborne microorganisms. Electrostatic charge can influence the bacteria's membrane potential (Cevc, 1990), which is crucial for their metabolic activities (Thomas *et al.*, 2011). Changes in membrane potential can affect ion transporters, channels, and essential proteins like ATPase, potentially rendering the microbes nonviable (Bond, 2000). Additionally, the process of charging can remove fragments of the bacterial surface and counter ions, further impacting their viability (Mainelis, 2001).

There is a correlation between membrane fluidity (which is related to membrane potential) and the reduction in airborne survival for bacteria during both aerosolization and airborne states (Ng *et al.*, 2018). Since bacteria often carry an electrostatic charge on their external walls, they can interact with electric fields, which affects their mobility and ability to colonize surfaces, including in forming biofilms (Chong *et al.*, 2021). Electrical charge on bacteria may also influence their role as ice and cloud condensation nuclei (Lukas *et al.*, 2020).

The natural electrostatic charge carried by microorganisms can be modified by external charges added during their dispersal by natural (e.g., wind) or artificial (e.g., aerosolization) processes or due to continuous bombardment by atmospheric ions. Triboelectric processes (e.g., the generation of electric charge through friction) during microorganism dispersal tend to impart high levels of bipolar charge (Mainelis *et al.*, 2002) (Table 5.2); this process seems to affect the more sensitive gram-negative bacteria rather than gram-positive bacterial spores. The airborne ions affect not only the overall charge level but also negatively affect the viability of both gram-negative and gram-positive bacteria, as shown in laboratory studies as early as 1964 and in more detail later (Phillips *et al.*, 1964; Comini *et al.*, 2021). Air ions were also shown to be effective against airborne bacteriophages (Trouwborst *et al.*, 1972). These experiments served as the basis for positing that atmospheric ions inactivate bioaerosols (Mohr, 2007).

Thus, once airborne microorganisms acquire a charge, their movement would be affected by external electrical fields and charges, like those created by power lines (Swanson and Jeffers, 1999) and thunderstorms. It has been suggested that strong electric fields during thunderstorms help uplift microorganisms to high altitudes, thereby explaining their presence at stratospheric altitudes of 40 km and above (Dehel *et al.*, 2008). However, atmospheric ions also tend to neutralize particles over time as the particles "age" which suggests that bioaerosols that spend considerable time aloft will tend to have low or neutral electrostatic charges, which will affect not only their motion but also metabolic functions (i.e., membrane potential).

Despite the importance of electrostatic charge for microorganism viability and interaction with the environment, there are only a limited number of laboratory and field studies on charge levels. It was shown that freshly aerosolized microorganisms in a laboratory could carry a substantial amount of electrical charge, up to several thousands of elementary charge units, sometimes exceeding 10,000 elementary electric charges (Mainelis *et al.*, 2002). The same work has shown the effects of bacterial viability. Sensitive bacteria like *Pseudomonas fluorescens*, carrying a net charge from –4,100 to +30 elementary charges, had 40-60% viability, but those with >2,700 positive charges had less than 1.5% viability (Table 5.2). Interestingly, the viability of stress-resistant spores like *B. subtilis* was not affected by these charge levels.

A study of 31 species of Agaricomycetes (fungi) found that immediately after their natural dispersal, spores carried from 10 to more than 1,000 elementary charges, depending on species, with net positive charge being prevalent (Saar and Salm, 2014) (Table 5.1).

As bioaerosols age, the initially imparted charge levels dissipate due to atmospheric ions and humidity. The above study on fungi calculated that a spore charge would dimmish sevenfold after 47 min (Saar and Salm, 2014). Still, a sufficient level of charge remains to affect microorganism travel under the effect of electrostatic fields, even, as mentioned, to lift them to stratospheric altitudes (Dehel *et al.*, 2008).

The airborne bacteria and fungi found in the ambient environment carry sufficient charge for their capture indoors and outdoors by electrostatic precipitation without imparting any additional charge (Yao and Mainelis, 2006) (typical electrostatic collection imparts additional charge on microorganisms). Using a similar experimental apparatus, it was shown that 93% of *B. subtilis* var *niger* aerosols carry 13–42 negative

charge units, while 5% carried a negative charge level of 42–195 or higher, while most of the *P. fluorescens* aerosols carried a negative charge level of 14–34 elementary units (Xie *et al.*, 2011) (Table 5.2). However, positive charge levels were not investigated.

Wei *et al.* (2014) measured charge levels of bacterial aerosol indoors and outdoors and found that outdoor culturable bacterial aerosol charges were normally distributed with a peak around 21–29 elementary charge units, while the indoor ones seemed to be skewed toward 46–92 elementary charge units (Table 5.1). However, the used experimental apparatus had limited resolution to detect the difference confidently. Still, other studies indicate that most airborne microorganisms tend to have a net negative charge in many environments (Lee *et al.*, 2004). Yet in some environments, especially outdoors, culturable bacteria of both polarities had a similar presence (Shen *et al.*, 2013).

Like bacteria and fungi, viruses are likely to carry electrical charges when airborne. However, the specific charge characteristics may vary depending on the virus type and environmental conditions. Like for bacteria, the amount of electric charge carried by airborne viruses can vary widely, potentially depending on factors such as the dispersal method and environmental conditions. The electrical charge on airborne viruses likely affects their behavior in air, including dispersal patterns, coagulation, and interactions with surfaces or other particles (Zhang *et al.*, 2016).

Electrostatic fields

The survival and multiple crucial functions of bacteria are affected by their membrane potential (Benarroch and Asally, 2020), which could be influenced by changes in electrical charges. These changes can disrupt basic metabolic activities, leading to reduced viability. Naturally, the motion and deposition of particles carrying electrostatic charges, including bioaerosols, could be affected by external electrostatic fields. It has even been suggested that micron-scale particles can be elevated to stratospheric altitudes due to the irradiation of particles by sunlight through gravitophotophoretic effects and electrostatic levitation (Dassarma *et al.*, 2020), and strong electrostatic fields created by thunderstorms (Dehel *et al.*, 2008).

Cell membranes become charged like a capacitor when exposed to an electric field. If the induced transmembrane potential exceeds about 1 V, it can cause irreversible damage and cell death (Beretta *et al.*, 2019). The killing effect depends on electric field strength, duration of exposure, microorganism type, and the medium composition (e.g., pH), where the microorganisms are suspended (Grahl and Märkl, 1996). While the effect of pH is more relevant to liquid media, it could play a role if an airborne microorganism is suspended within a droplet when exposed to an electrostatic field. Due to the ability of external electric fields to affect microorganisms, such fields have a long history of application in electroporation (Delorme, 1989; Tsong, 1991), electrotransformation (Chen *et al.*, 2024), and also to disinfect liquids (Gusbeth *et al.*, 2024).

In general, vegetative cells are much more susceptible to electric field damage than bacterial endospores or fungal ascospores (Grahl and Märkl, 1996). As per the same reference, it seems that for each cell type, there is a specific critical electric field strength and critical treatment time above which survival rates drop dramatically. Fields up to 25 kV/cm have been shown to have lethal effects on various species of vegetative bacteria and yeasts (Sale and Hamilton, 1967). Pulsed electric fields can

reduce living cell counts of vegetative cells by over 99.99% (Grahl and Märkl, 1996), and this method is effective against various bacteria and fungi suspended in liquids (Garner, 2019). On the other hand, weak electric fields can seemingly stimulate bacterial activity and increase cell mobility without causing damage and can even stimulate microbial activity for environmental cleanup (Beretta *et al.*, 2019).

While the intentional application of electroporation and electrotransformation is confined to laboratory studies, the effects of electrostatic fields on the motion and survival of airborne microorganisms have also been explored.

More than 90% of the *P. fluorescens* cells deposited on the surface of nonconductive filters were inactivated when fields of 15 kV/cm were applied for 30 min or longer; similar effects were observed when the same bacteria were exposed to weaker fields of 5 and 10 kV/cm but for 2 h. In contrast, the hardy *B. subtilis* var. *niger* cells subjected to the same treatment did not lose viability (Yao *et al.*, 2005). The same study exposed airborne *P. fluorescens* to 10 kV/cm for 30 s, but did not observe a substantial reduction in culturability (Yao *et al.*, 2005) (Table 5.2). Exposure of microorganisms in the airborne state to stronger electrostatic fields in laboratory conditions is challenging due to the dielectric breakdown of the air and the removal of these charged microorganisms from the air due to electrostatic precipitation caused by the applied field.

Non-enveloped (Ad5) and enveloped (SARS-CoV-2 pseudotyped lentivirus) viruses were subjected to electrostatic precipitation and more than 99% of them were inactivated by fields exceeding 10 kV/cm (Preston *et al.*, 2023). However, the authors do not differentiate whether the inactivation was achieved by charging or electrostatic fields. They also did not discuss the role of ozone, which is typically created during electrode discharge. Pulsed corona was also shown to be effective against airborne *P. fluorescens* and *Bacillus cereus* bacteria (Heesch *et al.*, 2000). Pulsed corona is unlikely to be encountered in the atmosphere unless purposefully created on a large scale. Corona discharges and non-thermal plasma, which are similar to those produced by lightning, except having a much lower temperature and electrical current, are also known to inactivate airborne microorganisms (Li *et al.*, 2024; Timoshkin *et al.*, 2012). Such corona discharges can be created by very high voltage transmission lines (Zaitsev and Kuchanskyy, 2021).

Near the Earth's surface, the typical electric field strength is about 100 V/m directed downward (positive charges move toward the ground). The field strength decreases with altitude, falling to about 5 V/m at an altitude of 10 km (American Meteorological Society[4]). On the other hand, very strong electrostatic fields could be created in the atmosphere during lightning. The maximum electric field that dry air can withstand without a dielectric breakdown is approximately 3 MV/m (30 kV/cm) under ideal conditions at atmospheric pressure (Rigden, 1996); in practice, this threshold is much lower.

During storms, ionized channels are formed between clouds or between clouds and Earth, and the voltage difference can reach 100 MV, corresponding to 16 kV/m and up to 700 kV/m due to the tip effect (Blanchard, 2013). At the point of lightning impact, most microorganisms are likely destroyed (Gary, 1999) due to high energy discharge.

4. American Meteorological Society (2024), Atmospheric electric field: https://glossary.ametsoc.org/wiki/Atmospheric_electric_field.

However, the created electrostatic fields outside the main channel are of similar strength to those used in electroporation (6 kV/cm – 12.5 kV/cm). It was suggested that lightning could act as an *in situ* "electroporator" and might mediate the transfer and acquisition of new genetic material by environmental microorganisms (Blanchard, 2013; Demanèche *et al.*, 2001). Moreover, it has been suggested that bacteria involved in forming ice nuclei, such as *P. syringae*, may be involved in triggering lightning in clouds and the associated electric field pulses of a few kV/cm (Gonçalves *et al.*, 2012; Nucci *et al.*, 1988), leading to the postulate that natural electrotransformation of bacteria might take place in clouds (Blanchard, 2013). Interestingly, based on laboratory experiments, it was suggested that ice crystals formed as part of ice nuclei could protect *P. syringae* cells from lightning discharge. The low density of these bacteria in clouds did not negatively affect their ability to survive electric shocks. For comparison, *E. coli*, one of the most electrotransformable strains, was not protected by ice nucleating activity and was less electrotransformed under low cell densities, in contrast to *P. syringae*. Among several considered species, *P. syringae* appeared to be the best adapted for survival and for being genetically electrotransformed in clouds, including during its transport.

Non-speciated particulate matter

Substantial microbial diversity could be found in the troposphere, with most microorganisms attached to particulate matter (PM). In fact, the attachment of microorganisms to PM aids in their dispersal, including over long distances (Chen *et al.*, 2020). Attachment of microorganisms to surfaces provided by other aerosol particles is likely to influence their viability and survival (Fröhlich-Nowoisky *et al.*, 2016), both negatively and positively. On the one hand, high concentrations of various chemicals in PM can inhibit the growth of attached microorganisms. This is particularly evident during heavy pollution days. On the other hand, moderate pollution could provide suitable microenvironments and nutrition to increase airborne microorganism survival (Chen *et al.*, 2020). It has even been suggested that airborne microbial species exhibit AQI (Air Quality Index)-dependent dynamics (Qin *et al.*, 2020). A similar observation was made by Gong *et al.* (2020), who found that a ratio of non-viable to total airborne bacteria increased when AQI increased from <50 to >200. On the other hand, Dong *et al.* (2016) showed a positive correlation between total airborne microorganism concentration and $PM_{2.5}$ as well as AQI, especially during hazy days compared to non-hazy days.

The effect of non-speciated PM on airborne microorganisms has been explored in laboratory experiments as well. Microorganisms collected on filters in a polluted atmosphere ($PM_{2.5}$ ~ 250 μg/m^3) had faster decay rates, more bacterial diversity, and less diverse fungal community compared to samples collected from a cleaner environment ($PM_{2.5}$ <75 μg/m^3) (Xu *et al.*, 2021). Another study exposed the airborne wild-type *E. coli* K12 (JM109) and its modified version JM109-pEC958 to Arizona Road Dust ranging from 250 to 2000 μg/m^3 and found that their viability progressively decreased to 13% and 60%, respectively (Agarwal *et al.*, 2024) (Table 5.2). The authors suggested that mineral dust, organic matter, ROS, and other pollutants reduced bacterial viability.

On the other hand, PM could also offer protection from environmental stressors. Laboratory experiments with airborne *M. smegmatis* captured on filters at different concentrations of airborne soot indicated that higher soot concentrations offered

increased protection against UV (Noda *et al.*, 2022) (Table 5.2). Particles can also provide a shielding effect for viruses. For example, the survival ability of the gastroenteritis virus, the swine influenza virus, and the avian influenza virus was lower on 100-200 nm particles compared to viruses carried by 300-450 nm particles (Zuo *et al.*, 2013), presumably due to a protective effect of larger particles.

The nature of the PM also plays a role. The survival of airborne bacteria aerosolized with sludge dust from the coastal area of Japan was significantly higher than when aerosolized with Mongolian desert dust, while soot seemingly had a protective role (Noda *et al.*, 2019) (Table 5.2). As mentioned in an earlier section, growth substrates such as sugars can also be present in particles. Since aerosol particles may and often do contain water (Ervens *et al.*, 2024), the water uptake by bacteria may be enabled by the formation of biosurfactants (Gill *et al.*, 1983), thus facilitating the survival of microorganisms in the air. This would be especially relevant for bioaerosols originating from water sources.

Sampling of fire smoke aerosols above wildland fires indicated that fire smoke could serve as a source of viable and diverse microbial aerosols with bacterial cell concentrations of 10^4-10^5/m^3 (Kobziar *et al.*, 2022; Moore *et al.*, 2020), and having much higher taxon richness compared to ambient air (Kobziar *et al.*, 2022). Seemingly, the combustion environment selects for resilient and rich taxa while aiding their dispersal on a global scale (Kobziar *et al.*, 2022). In addition, smoke constituents like soot and ash, could offer protection to microorganisms by shielding them from UV, desiccation, and oxidative stress further aiding dispersal of viable microorganisms.

The physical size of a particle or agglomerate to which microorganisms are attached could also affect its survival because larger bioaerosols settle faster, reducing the duration of their exposure to environmental stressors.

⏩ Residence time aloft

One variable that ties various stressors and growth enhancing compounds is microorganism residence time in the atmosphere. The longer the residence time, the longer the microorganisms will be affected by the discussed stressors, thus minimizing their chance of survival. In addition, atmospheric ions tend to neutralize electrostatic changes on particles over time, thus possibly affecting not only their motion, but also their metabolic function. However, some organisms, such as spore-formers can survive longer due to protective adaptations. On the other hand, longer times aloft in nutrient-rich microenvironments offers microorganisms a better chance not only to maintain their viability, but also to grow.

The residence time and the resulting survival of airborne microorganisms is governed by the species, their atmospheric insertion method and resulting altitude, aerodynamic size, and atmospheric conditions (Haenel *et al.*, 2015), including air currents, wind patterns, and the structure of the boundary layer.

The estimated residence times vary widely, depending on the factors mentioned above. It was estimated that 50% of microbes detected in the boundary layer over North Atlantic were still airborne 12 days later allowing them to travel up to 12,000 km (Mayol *et al.*, 2017). The residence time in boundary layer is sufficient for intercontinental dispersal of bacteria and archaea by transpacific winds (Smith *et al.*, 2013), including transfer of viable human pathogens by 2000 km (Rodó *et al.*, 2024).

Since settling velocities of 1-2 μm particles, including bacteria, due to gravity are very low, residence times at higher altitudes could be substantial (Bryan *et al.*, 2019). However, the microorganism removal could be much faster due to stratospheric intrusions (Lin *et al.*, 2015). Still, some-desiccation tolerant bacteria can survive for up to 140 days (Bryan *et al.*, 2019). On the other hand, as discussed above, laboratory studies show that some microorganisms are inactivated by atmospheric stressors within a few hours (Smith *et al.*, 2011) or even much faster, depending on atmospheric temperature and RH (Ghosh *et al.*, 2015; Tang, 2009).

In summary, the existing observations of viable microorganisms at higher altitudes, including stratosphere, offer a possibility that some microorganisms may survive the harsh atmospheric conditions, including outside of protective water environment. The residence time could be prolonged by horizontal and vertical transport provided by air currents and, as mentioned elsewhere in this chapter, electrostatic fields.

⏩ Summary

Air is a very different environment than soil or water, and life in the atmosphere outside of water droplets must be challenging for microorganisms. To date, it has not been shown whether abundant microbial activity in the ambient air (outside cloudwater, fog, or rain) is widespread or biogeochemically significant. Despite multiple environmental stressors (Table 5.1) that could lead to microorganisms' loss of culturability and even death (Figure 5.2), atmospheric chemists consistently find chemicals in cloud and aerosol samples that are also known to be microbial metabolic products (Ervens *et al.*, 2011). Further, live microbes from taxa known to be capable of metabolizing atmospheric VOCs have been collected from air in the upper troposphere, suggesting long-lived potential for biological turnover of carbon and nutrients in the atmosphere (Deleon-Rodriguez *et al.*, 2013). It is not yet known exactly how concurrent complex multiphase abiotic chemical reactions and microbial activity interact in the atmosphere. In intriguing field studies of the atmosphere, increased 16S rRNA content of specific taxa has been extended as a method for evaluating activity of specific members of the assemblage (Péguilhan *et al.*, 2024; Šantl-Temkiv *et al.*, 2018). Laboratory studies indicate that there are clear differences in airborne survival for certain organisms, for instance, *S. pyogenes* survived the airborne state better than *E. coli* MRE162. It was speculated that this was due to *S. pyogenes* being more tolerant of ROS (Oswin *et al.*, 2023; Oswin *et al.*, 2024). There are difficulties assessing the response of aerial microbes to their environment both in the field and in laboratory studies. The most comprehensive laboratory study observing the effect of different atmospheric stressors/open-air factors on *E. coli* K12 was done by Kinahan *et al.* (2019). Although viability was decreased when exposed to different chemical stressors, the exact cellular response (e.g., transcriptomic or proteomic response) to different stressor combinations was not investigated.

Much of the laboratory work has focused on survival or conversely inactivation of respiratory viruses (e.g., SARS-CoV-2) and model bacteria (e.g., *E. coli* or *P. syringae*). However, the airborne microbial world is incredibly diverse, and experiments with a limited number of species, even if considered model species, likely offer an incomplete understanding of the effects that environmental stressors impose on bioaerosols. At the local scale, airborne microbial makeup varies substantially over a period of

minutes, hours, or days, and represents a highly dynamic and heterogeneous environment. Although many of the core cellular responses to chemical and physical stress or availability of growth substrates are conserved across microorganisms, the physiological diversity amongst microorganisms may result in different interactions within a multiphasic aerosol droplet or particle.

Research discussed above has indicated stressors and their concentrations or strengths that negatively affect airborne microbes, but exposure to persistent low concentrations and combinations of stressors affect cells in unknown ways and require further investigation, especially given indications that a combination of chemical stressors achieves stronger inactivation than each stressor individually (Kinahan *et al.*, 2019; Truyols-Vives *et al.*, 2024). Further, in the air, single microorganisms or microorganisms attached to carrier particles have low spatial densities (i.e., low number concentrations) and are unlikely to experience interspecies interactions that occur in soils, sediments or aquatic environments. However, it has been suggested that those microorganisms that are co-localized in aerosol particles may have some type of interactions that promote their survival (David *et al.*, 2024). This adds another variable that researchers should consider when investigating bioaerosols and the impact of atmospheric physicochemical stressors on them.

Based upon the results of published studies cited and reviewed here, the major open-air factors/stressors have been grouped into three categories: typically adverse, conditionally adverse, and potential enhancer (Figure 5.2). As discussed earlier in this chapter, each of the parameters listed impacts bioaerosols. Overall, high concentrations/amounts of the typically adverse parameters lead to an increased inactivation/death of bioaerosols. The conditionally adverse parameters are often beneficial or harmful to the bioaerosols, depending on their concentrations or values, as discussed earlier. Finally, the potential enhancers, mainly growth substrates, may make the atmosphere a more hospitable environment for bioaerosols, but this requires intense further research. The effect of some environmental stressors, e.g., UV and humidity or temperature and humidity, has been examined in more detail due to their potential application to minimize the spread of infectious diseases. The effect of other physical stressors, such as electrostatic fields and charges, at environmentally relevant levels remains only minimally explored. The role of multiple growth-enhancing substances in bioaerosol survival and metabolic activity outside of cloud droplets also remains underexplored despite its clear impact on atmospheric processes. The effect of interaction among multiple stressors and growth enhancers and their role on airborne microorganisms could be added to the list of items that need to be explored further.

Given all of this, the interplay between the growth-enhancing substances and chemical and physical stressors (see Table 5.1 for concentrations, and Table 5.3 for a summary of concentrations) that airborne microorganisms face will dictate their survival and fate (Figure 5.2). If these microorganisms are given sufficient resources/nutrients and enough time while aloft, they could not only maintain their viability but also grow. If microorganisms do not receive appropriate nutrients, they might not grow but still be able to maintain viability and culturability. If the culturable microorganisms experience adverse conditions caused by one or more stressors/open air factors discussed here, then they may lose their culturability,

while maintaining viability. Finally, if the lack of nutrients and presence of stressors overwhelm the microorganisms' ability to survive, they will lose their viability and die (Figure 5.2).

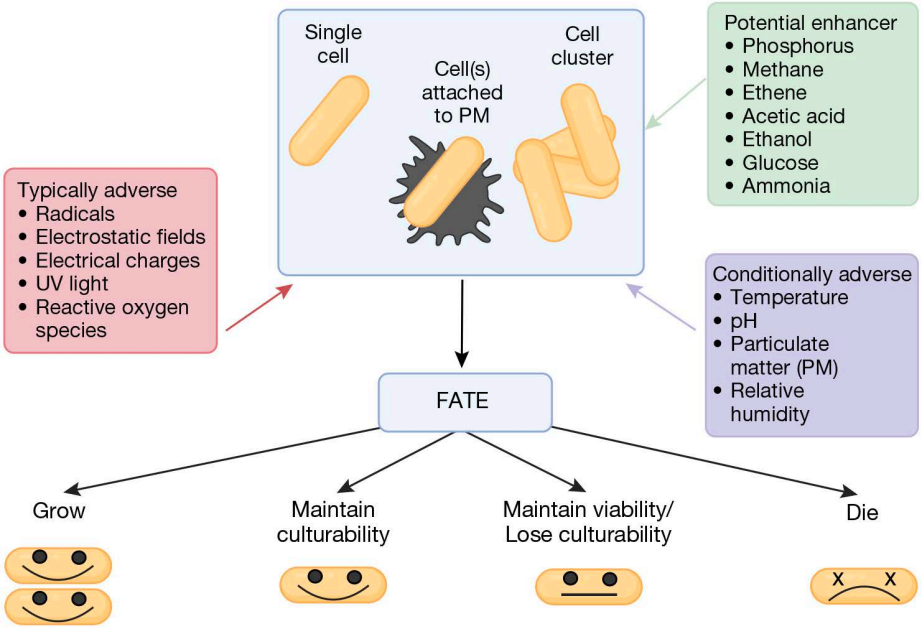

Figure 5.2. Fate of airborne microorganisms.

Due to the diversity and concentrations of open-air factors and atmospheric stressors, airborne microorganisms are exposed to numerous conditions/factors that can be considered as typically adverse, conditionally adverse, or potential enhancers. Overall, the combinations of these factors will dictate whether an airborne microorganism will grow, maintain its culturability, maintain viability/lose its culturability, or die. © Dillon K. (2025); created in BioRender (https://BioRender.com/28qmapj).

It is necessary to bridge the knowledge gaps between lab-based studies that mechanistically determine the effect of stressors on bioaerosols and environmental monitoring results. There needs to be a mechanistic investigation of the components of open-air factors so that we can gain a better understanding of the limits on microbial aeolian dispersal. By understanding the major influences upon microbial survival and functioning, the role of the atmosphere in microbial evolution can be better understood, inform our understanding of the atmosphere as a dispersal vector, and inform the public health risks associated with microbial aerosols. Despite the unique nature of the atmosphere as a microbial environment, Womack *et al.* (2010) have proposed the intriguing hypothesis that there could be global, biogeographically distinct aerial ecosystems based on the various compartments that exist in Earth's atmosphere. Evidence suggests that active airborne microbes may be an important missing element in our studies of the atmosphere and that despite the adverse effect of chemical and physical stressors, presence of substrates and nutrients could enhance their survival or even growth. All these considerations provide impetus to continue and expand research into the presence, survival, and propagation of microorganisms in the troposphere and even the stratosphere.

Table 5.3. Summary of environmental factors and their magnitudes affecting airborne microorganisms.

Parameter	Concentration (units)
Growth substrates and Nutrients	
Methane	1.9 – 250,000 ppm
Ethene	0.002 – 268 ppb
Ethanol	0.02 – 2176 ppb
Acetic acid	0.4 – 25,000 ppb
Glucose	0.1 – 22,210 ng/m^3
Ammonia	<1 ppb – 24 ppb
Total phosphorus	0.6 – 2200 ng/m^3
Chemical Factors	
pH	4 – 7
Ozone	~0 – 100 ppb
OH radicals	~10^6 radicals/cm^3
H_2O_2	0.1 – 2 >4 ppbv
Metals (Zn, Fe, Cu)	0.071 – 2252.9 µg/m^3
Salts (Na)	0.178 – 21.7 µg/m^3
Physical Factors	
Temperature	-60 – 40°C
RH	0 – 2100%
UV	0.17 – 20.83 J/$m^2{}_{254}$/min
Electrostatic charges	0 – 2 ± 10,000 elementary charges
Electrical fields	5 – 30,000 V/m
Particulate matter	0 – 2 >300 µg/m^3
Residence time aloft	0 – 2140 days

Literature cited

Abd Aziz A., *et al.*, 2018. Comparative study of the airborne microbial communities and their functional composition in fine particulate matter ($PM_{2.5}$) under non-extreme and extreme $PM_{2.5}$ conditions. *Atmospheric Environment*, 194, 82-92. https://doi.org/10.1016/j.atmosenv.2018.09.027

Abichou T., *et al.*, 2023. Estimation of total landfill surface methane emissions using geospatial approach combined with measured surface ambient air methane concentrations. *J. Air Waste Manag. Assoc.*, 73 (12), 902-913. https://doi.org/10.1080/10962247.2023.2271431

Adhikari A., *et al.*, 2006. Correlation of ambient inhalable bioaerosols with particulate matter and ozone: A two-year study. *Environ. Pollut.*, 140, 16-28. https://doi.org/10.1016/j.envpol.2005.07.004

Aganovic A., *et al.*, 2022. Modeling the impact of indoor relative humidity on the infection risk of five respiratory airborne viruses. *Sci. Rep.*, 12 (1), 11481. https://doi.org/10.1038/s41598-022-15703-8

Agarwal V., *et al.*, 2024. Influence of CO_2 and dust on the survival of non-resistant and multi-resistant airborne *E. coli* strains. *Antibiotics*, 13 (6), 558. https://doi.org/10.3390/antibiotics13060558

Ai Y., *et al.*, 2022. Characterization of single fungal aerosol particles in a reactive atmospheric environment using timeresolved optical trapping-Raman spectroscopy (OT-RS). *Environ. Sci.: Atmos.*, 2, 591-600. https://doi.org/10.1039/D2EA00030

Alsved M., *et al*., 2020. Natural sources and experimental generation of bioaerosols: Challenges and perspectives. *Aerosol Sci. Technol.*, 54 (5), 547-571. https://doi.org/10.1080/02786826.2019.1682509

Alsved M., *et al*., 2018. Effect of aerosolization and drying on the viability of *Pseudomonas syringae* cells. *Front. Microbiol.*, 9, 3086. https://doi.org/10.3389/fmicb.2018.03086

Altuzar V., *et al*., 2005. Atmospheric ethene concentrations in Mexico City: Indications of strong diurnal and seasonal dependences. *Atmospheric Environment*, 39 (29), 5219-5225. https://doi.org/10.1016/j.atmosenv.2004.10.002

Alvarez L.A., *et al*., 2009. Characterization of marine isoprene-degrading communities. *Environ. Microbiol.*, 11 (12), 3280-3291. https://doi.org/10.1111/j.1462-2920.2009.02069

Amato P., *et al*., 2017. Active microorganisms thrive among extremely diverse communities in cloud water. *PLoS One*, 12 (8), e0182869. https://doi.org/10.1371/journal.pone.0182869

Amato P., *et al*., 2023. The aeromicrobiome: The selective and dynamic outer-layer of the Earth's microbiome. *Front. Microbiol.*, 14, 1186847. https://doi.org/10.3389/fmicb.2023.1186847

Angle K., *et al*., 2021. Acidity across the interface from the ocean surface to sea spray aerosol. *Proc. Natl Acad. Sci. USA,* 118 (2), e2018397118. https://doi.org/10.1073/pnas.2018397118

Archer S.D., Pointing S.B., 2020. Anthropogenic impact on the atmospheric microbiome. *Nat. Microbiol.*, 5 (2), 229-231. https://doi.org/10.1038/s41564-019-0650-

Astals S., *et al*., 2018. Characterising and modelling free ammonia and ammonium inhibition in anaerobic systems. *Water Res.*, 143, 127-135. https://doi.org/10.1016/j.watres.2018.06.021

Azua-Bustos A., *et al*., 2014. Gloeocapsopsis AAB1, an extremely desiccation-tolerant cyanobacterium isolated from the Atacama Desert. *Extremophiles*, 18 (1), 61-74. https://doi.org/10.1007/s00792-013-0592-

Bailey R., *et al*., 2007. Effect of ozone and open air factor against aerosolized *Micrococcus luteus*. *J. Food Prot.*, 70 (12), 2769-2773. https://doi.org/10.4315/0362-028X-70.12.2769

Baker A.K., *et al*., 2008. Measurements of nonmethane hydrocarbons in 28 United States cities. *Atmos. Environ.*, 42 (1), 170-182. https://doi.org/10.1016/j.atmosenv.2007.09.007

Balasubramanian R., Husain L., 1997. Observations of gas-phase hydrogen peroxide at an elevated rural site in New York. *J. Geophys. Res. Atmos.*, 102 (D17), 21209-21220. https://doi.org/10.1029/97JD01480

Barbaro E., *et al*., 2015. Sugars in Antarctic aerosol. *Atmos. Environ.*, 118, 135-144. https://doi.org/10.1016/j.atmosenv.2015.07.047

Behera S.N., *et al*., 2013. Ammonia in the atmosphere: A review on emission sources, atmospheric chemistry and deposition on terrestrial bodies. *Environ. Sci. Pollut. Res. Int.*, 20, 8092-8131. https://doi.org/10.1007/s11356-013-2051-

Ben-David A., Sagripanti J.-L., 2010. A model for inactivation of microbes suspended in the atmosphere by solar ultraviolet radiation. *Photochem. Photobiol.*, 86 (4), 895-908. https://doi.org/10.1111/j.1751-1097.2010.00738

Benarroch J.M., Asally M., 2020. The microbiologist's guide to membrane potential dynamics. *Trends Microbiol.*, 28 (4), 304-314. https://doi.org/10.1016/j.tim.2019.12.008

Bender M., Conrad R., 1992. Kinetics of CH_4 oxidation in oxic soils exposed to ambient air or high CH_4 mixing ratios. *FEMS Microbiol. Lett.*, 101 (4), 261-270. https://doi.org/10.1111/j.1574-6968.1992.tb05783

Beretta G., *et al*., 2019. The effects of electric, magnetic and electromagnetic fields on microorganisms in the perspective of bioremediation. *Reviews in Environmental Science and Bio/Technology*, 18 (1), 29-75. https://doi.org/10.1007/s11157-018-09491-

Berlett B., Stadtman E., 1997. Protein oxidation in aging, disease, and oxidative stress. *J. Biol. Chem.*, 272 (33), 20323-20316. https://doi.org/10.1074/jbc.272.33.20313

Beygi Z., *et al*., 2011. Oxidation photochemistry in the Southern Atlantic boundary layer: Unexpected deviations of photochemical steady state. *Atmos. Chem. Phys.*, 11, 8497-8513. https://doi.org/10.5194/acp-11-8497-2011

Blanchard L., 2013. Impact of lightning on evolution, structure and function of bacterial communities, PhD Thesis, Ecole Centrale de Lyon. https://theses.hal.science/tel-01024190

Bond D.R.a.R., J.B., 2000. Protonmotive force regulates the membrane conductance of Streptococcus bovis in a non-ohmic fashion. *Microbiology*, 146 (Pt3), 687-694. https://doi.org/10.1099/00221287-146-3-687

Bono N., *et al*., 2021. Effect of UV irradiation and TiO_2-photocatalysis on airborne bacteria and viruses: An overview. *Materials*, 14 (5), 1075. https://doi.org/10.3390/ma14051075

Borhani F., *et al*., 2023. Current status and future forecast of short-lived climate-forced ozone in Tehran, Iran, derived from ground-based and satellite observations. *Water Air Soil Pollut.*, 234, 134. https://doi.org/10.1007/s11270-023-06138-

Brickner P.W., *et al*., 2003. The application of ultraviolet germicidal irradiation to control transmission of airborne disease: Bioterrorism countermeasure. *Public Health Reports*, 118 (2), 99-114. https://doi.org/10.1093/phr/118.2.99

Bruhwiler L., *et al*., 2021. The Arctic carbon cycle and its response to changing climate. *Current Climate Change Reports*, 7, 14-34. https://doi.org/10.1007/s40641-020-00169-

Bryan N.C., *et al*., 2019. Abundance and survival of microbial aerosols in the troposphere and stratosphere. *ISME J.*, 13 (11), 2789-2799. https://doi.org/10.1038/s41396-019-0474-

Busse H.-J., *et al*., 2003. *Sphingomonas aurantiaca* sp. nov., *Sphingomonas aerolata* sp. nov. and *Sphingomonas faeni* sp. nov., air-and dustborne and Antarctic, orange-pigmented, psychrotolerant bacteria, and emended description of the genus Sphingomonas. *Int. J. Syst. Evol. Microbiol.*, 53 (5), 1253-1260. https://doi.org/10.1099/ijs.0.02461-

Cape J.N., *et al*., 2011. Nitrogen processes in the atmosphere. *The European Nitrogen Assessment: Sources, Effects and Policy Perspectives*, 177. https://doi.org/10.1017/CBO9780511976988.012

Casanova L.M., *et al*., 2010. Effects of air temperature and relative humidity on Coronavirus survival on surfaces. *Appl. Environ. Microbiol.*, 76 (9), 2712-2717. https://doi.org/10.1128/AEM.02291-09

Caulton D.R., *et al*., 2014. Toward a better understanding and quantification of methane emissions from shale gas development. *Proc. Natl Acad. Sci. USA*, 111 (17), 6237-6242. https://doi.org/10.1073/pnas.1316546111

Cevc G., 1990. Membrane electrostatics. *Biochimica et Biophysica Acta (BBA)-Reviews on Biomembranes*, 1031 (3), 311-382. https://doi.org/10.1016/0304-4157(90)90015-

Chai A., *et al*., 2023. Effect of temperature and humidity on dynamics and transmission of *Pseudomonas amygdali* pv. lachrymans aerosols. *Front. Plant Sci.*, 14. https://doi.org/10.3389/fpls.2023.1087496

Chance R., *et al*., 2015. Atmospheric trace metal concentrations, solubility and deposition fluxes in remote marine air over the south-east Atlantic. *Mar. Chem.*, 177, 45-56. https://doi.org/10.1016/j.marchem.2015.06.028

Chandrangsu P., *et al*., 2017. Metal homeostasis and resistance in bacteria. *Nat. Rev. Microbiol.*, 15, 338-350. https://doi.org/10.1038/nrmicro.2017.15

Chapman S., 1930. On ozone and atomic oxygen in the upper atmosphere. *London, Edinburgh Dublin Phil. Mag. J. Sci.*, 10 (64), 369-383. https://doi.org/10.1080/14786443009461588

Cheluszka P., *et al*., 2023. The spread of microbiota in the air of an underground hard coal mine – A case study. *Building and Environment*, 242, 110495. https://doi.org/10.1016/j.buildenv.2023.110495

Chen W., *et al*., 2024. Electrotransformation of foodborne pathogen *Cronobacter sakazakii* by a simple method. *Foodborne Pathog. Dis.*, 21 (1), 61-67. https://doi.org/10.1089/fpd.2023.0048

Chen X., *et al*., 2020. A Review on airborne microbes: The characteristics of sources, pathogenicity and geography. *Atmosphere*, 11 (9), 919. https://doi.org/10.3390/atmos11090919

China S., *et al*., 2018. Fungal spores as a source of sodium salt particles in the Amazon basin. *Nat Comm*, 9, 4793. https://doi.org/10.1038/s41467-018-07066-

Chong P., *et al*., 2021. How bacteria use electric fields to reach surfaces. *Biofilm*, 3, 100048. https://doi.org/10.1016/j.bioflm.2021.100048

Chulakadabba A., *et al*., 2023. Methane point source quantification using MethaneAIR: A new airborne imaging spectrometer. *Atmospheric Measurement Techniques*, 16 (23), 5771-5785. https://doi.org/10.5194/amt-16-5771-2023

Churchill S., *et al*., 1995. Sorption of heavy metals by prepared bacterial cell surfaces. *J. Environ. Eng.*, 121 (10), 706-711. https://doi.org/10.1061/(ASCE)0733-9372(1995)121:10(706)

Claiborn C., Aneja V., 1991. Measurements of atmospheric hydrogen peroxide in the gas phase and in cloud water at Mt. Mitchell, North Carolina. *J. Geophys. Res. Atmos.*, 96 (D10), 18771-18787. https://doi.org/10.1029/91JD00931

Clauß M., *et al.*, 2022. Development of a novel bioaerosol chamber to determine survival rates of airborne Staphylococci. *Atmosphere*, 13, 869. https://doi.org/10.3390/atmos13060869

Cleveland C.C., Yavitt J.B., 1998. Microbial consumption of atmospheric isoprene in a temperate forest soil. *Appl. Environ. Microbiol.*, 64 (1), 172-177. https://doi.org/10.1128/AEM.64.1.172-177.1998

Comini S., *et al.*, 2021. Positive and negative ions potently inhibit the viability of airborne gram-positive and gram-negative bacteria. *Microbiology Spectrum*, 9 (3), e00651-00621. https://doi.org/10.1128/Spectrum.00651-21

Coohill T.P., 1986. Virus-cell interactions as probes for vacuum-ultraviolet radiation damage and repair. *Photochem. Photobiol.*, 44 (3), 359-363. https://doi.org/10.1111/j.1751-1097.1986.tb04676

Cortesão M., *et al.*, 2021. MARSBOx: Fungal and bacterial endurance from a balloon-flown analog mission in the stratosphere. *Front. Microbiol.*, 12, 601713. https://doi.org/10.3389/fmicb.2021.601713

Cox C., Baldwin F., 1964. A method for investigating the cause of death of airborne bacteria. *Nature*, 202 (4937), 1135-1135. https://doi.org/10.1038/2021135a

Cox C., Goldberg L., 1972. Aerosol survival of *Pasteurella tularensis* and the influence of relative humidity. *Applied Microbiology*, 23 (1), 1-3. https://doi.org/10.1128/am.23.1.1-3.1972

Craig R., *et al.*, 2018. Direct determination of aerosol pH: Size-resolved measurements of submicrometer and supermicrometer aqueous particles. *Anal. Chem.*, 90, 11232-11239. https://doi.org/10.1021/acs.analchem.8b00586

Cutler T.D., Zimmerman J.J., 2011. Ultraviolet irradiation and the mechanisms underlying its inactivation of infectious agents. *Anim. Health Res. Rev.*, 12 (1), 15-23. https://doi.org/10.1017/S1466252311000016

Dall'osto M., *et al.*, 2019. Simultaneous detection of alkylamines in the surface ocean and atmosphere of the Antarctic sympagic environment. *ACS Earth Space Chem.*, 3, 854-862. https://doi.org/10.1021/acsearthspacechem.9b00028

Dall'osto M., *et al.*, 2020. Enrichment of organic nitrogen in primary biological particles during advection over the North Atlantic. *Atmos. Environ.*, 222, 117160. https://doi.org/10.1016/j.atmosenv.2019.117160

Dark F., Nash T., 1970. Comparative toxicity of various ozonized olefins to bacteria suspended in air. *J. Hyg. Camb.*, 68, 245-252. https://doi.org/10.1017/S0022172400028710

Dassarma P., Dassarma S., 2018. Survival of microbes in Earth's stratosphere. *Curr. Opin. Microbiol.*, 43, 24-30. https://doi.org/10.1016/j.mib.2017.11.002

Dassarma P., *et al.*, 2020. Earth's stratosphere and microbial life. *Curr. Issues Mol. Biol.*, 38 (1), 197-244. https://doi.org/10.21775/cimb.038.197

David S., *et al.*, 2024. Stability of influenza A virus in droplets and aerosols is heightened by the presence of commensal respiratory bacteria. *J. Virol.*, 98 (7), e00409-00424. https://doi.org/10.1128/jvi.01222-24

De Araujo G.G., *et al.*, 2019. Survival and ice nucleation activity of Pseudomonas syringae strains exposed to simulated high-altitude atmospheric conditions. *Sci. Rep.*, 9 (1), 7768. https://doi.org/10.1038/s41598-019-44283-

De Bont J., Albers R.A., 1976. Microbial metabolism of ethylene. *Antonie van Leeuwenhoek*, 42, 73-80. https://doi.org/10.1007/BF00399450

De Gouw J., *et al.*, 2009. Airborne measurements of ethene from industrial sources using laser photoacoustic spectroscopy. *Environ. Sci. Technol.*, 43 (7), 2437-2442. https://doi.org/10.1021/es802701

De Gouw J.A., *et al.*, 2012. Increasing atmospheric burden of ethanol in the United States. *Geophys. Res. Lett.*, 39 (15). https://doi.org/10.1029/2012GL052109

De La Puente M., Laage D., 2023. How the acidity of water droplets and films is controlled by the air–water interface. *J. Am. Chem. Soc.*, 145, 25186-25194. https://doi.org/10.1021/jacs.3c07506

Defratyka S.M., *et al*., 2021. Mapping urban methane sources in Paris, France. *Environ. Sci. Technol.*, 55 (13), 8583-8591. https://doi.org/10.1021/acs.est.1c00859

Dehel T., *et al*., 2008. Uplift of microorganisms by electric fields above thunderstorms. *Journal of Electrostatics*, 66 (9-10), 463-466. https://doi.org/10.1016/j.elstat.2008.04.014

Deleon-Rodriguez N., *et al*., 2013. Microbiome of the upper troposphere: Species composition and prevalence, effects of tropical storms, and atmospheric implications. *Proc. Natl Acad. Sci. USA,* 110 (7), 2575-2580. https://doi.org/10.1073/pnas.1212089110

Delmas R., *et al*., 1997. Global inventory of NOx sources. *Nutr. Cycl. Agroecosyst.*, 48, 51-60. https://doi.org/10.1023/A:1009793806086

Delorme E., 1989. Transformation of *Saccharomyces cerevisiae* by electroporation. *Appl. Environ. Microbiol.*, 55 (9), 2242-2246. https://doi.org/10.1128/aem.55.9.2242-2246.1989

Demanèche S., *et al*., 2001. Laboratory-scale evidence for lightning-mediated gene transfer in soil. *Appl. Environ. Microbiol.*, 67 (8), 3440-3444. https://doi.org/10.1128/AEM.67.8.3440-3444.2001

Desai G., *et al*., 2023. Efficacy of grignard pure to inactivate airborne phage ms2, a common SARS-CoV-2 surrogate. *Environ. Sci. Technol.*, 57 (10), 4231-4240. https://doi.org/10.1021/acs.est.2c08632

Diao X., *et al*., 2023. Atmospheric phosphorus and its geochemical cycling: Fundamentals, progress, and perspectives. *Earth-Science Reviews*, 104492. https://doi.org/10.1016/j.earscirev.2023.104492

Diaz F., *et al*., 2020. Ozone trends in the United Kingdom over the last 30 years. *Atmosphere*, 11, 534. https://doi.org/10.3390/atmos11050534

Dienhart D., *et al*., 2021. Measurement report: Observation-based formaldehyde production rates and their relation to OH reactivity around the Arabian Peninsula. *Atmos. Chem. Phys.*, 21, 17373-17388. https://doi.org/10.5194/acp-21-17373-2021

Dilbeck C., Finlayson-Pitts B., 2013. Hydroxyl radical oxidation of phospholipid-coated NaCl particles. *Phys. Chem. Chem. Phys.*, 15, 9833-9844. https://doi.org/10.1039/c3cp51237

Dill K., Shortle D., 1991. Denatured states of proteins. *Annu. Rev. Biochem.*, 60, 795-825. https://doi.org/10.1146/annurev.bi.60.070191.004051

Dillon K.P., *et al*., 2022. Characterization and DNA stable-isotope probing of methanotrophic bioaerosols. *Microbiology Spectrum*, 10 (6), e03421-03422. https://doi.org/10.1128/spectrum.03421-22

Dimmick R., *et al*., 1975. Evidence for metabolic activity of airborne bacteria. *J. Aerosol Sci.*, 6 (6), 387-393. https://doi.org/10.1016/0021-8502(75)90054-

Dimmick R., *et al*., 1979a. Evidence for more than one division of bacteria within airborne particles. *Appl. Environ. Microbiol.*, 38 (4), 642-643. https://doi.org/10.1128/aem.38.4.642-643.1979

Dimmick R.L., *et al*., 1979b. Evidence that bacteria can form new cells in airborne particles. *Appl. Environ. Microbiol.*, 37 (5), 924-927. https://doi.org/10.1128/aem.37.5.924-927.1979

Ding J., *et al*., 2019. Aerosol pH and its driving factors in Beijing. *Atmos. Chem. Phys.*, 19, 7939-7954. https://doi.org/10.5194/acp-19-7939-2019

Dong L., *et al*., 2016. Concentration and size distribution of total airborne microbes in hazy and foggy weather. *Sci. Tot. Environ*, 541, 1011-1018. https://doi.org/10.1016/j.scitotenv.2015.10.001

Druett H., May K., 1968. Unstable germicidal pollutant in rural air. *Nature*, 220, 395-396. https://doi.org/10.1038/220395a

Druett H., Packman L., 1968. Sensitive microbiological detector for air pollution. *Nature*, 218, 699. https://doi.org/10.1038/218699a

Duan C.S.,*et al*., 2023. The research hotspots and trends of volatile organic compound emissions from anthropogenic and natural sources: A systematic quantitative review (vol 216, 114386, 2023). *Environ. Res.*, 218. https://doi.org/10.1016/j.envres.2022.114386

Dubey P., *et al*., 2022. Ozonation: An evolving disinfectant technology for the food industry. *Food Bioproc. Tech.*, 15, 2102-2113. https://doi.org/10.1007/s11947-022-02876-

Dunklin E.W., Puck T.T., 1948. The lethal effect of relative humidity on air-borne bacteria. *J. Exp. Med.*, 87 (2), 87-101. https://doi.org/10.1084/jem.87.2.87

Dybwad M., Skogan G., 2017. Aerobiological stabilities of different species of gram-negative bacteria, including well-known biothreat simulants, in single-cell particles and cell clusters of different compositions. *Appl. Environ. Microbiol.*, 83 (18), e00823-00817. https://doi.org/10.1128/AEM.00823-17

Ehrlich R., *et al.*, 1970. Relationship between atmospheric temperature and survival of airborne bacteria. *Applied Microbiology*, 19 (2), 245-249. https://doi.org/10.1128/am.19.2.245-249.1970

Elbert W., *et al.*, 2007. Contribution of fungi to primary biogenic aerosols in the atmosphere: Wet and dry discharged spores, carbohydrates, and inorganic ions. *Atmos. Chem. Phys.*, 7 (17), 4569-4588. https://doi.org/10.5194/acp-7-4569-2007

Erkorkmaz B.A., *et al.*, 2023. Aerial transport of bacteria by dust plumes in the Eastern Mediterranean revealed by complementary rRNA/rRNA-gene sequencing. *Communications Earth & Environment*, 4 (1), 24. https://doi.org/10.1038/s43247-023-00679-

Ertem G., *et al.*, 2021. Evidence for the protection of N-heterocycles from gamma radiation by Mars analogue minerals. *Icarus*, 368, 114540. https://doi.org/10.1016/j.icarus.2021.114540

Ervens B., *et al.*, 2011. Secondary organic aerosol formation in cloud droplets and aqueous particles (aqSOA): A review of laboratory, field and model studies. *Atmos. Chem. Phys.*, 11 (21), 11069-11102. https://doi.org/10.5194/acp-11-11069-2011

Ervens B., *et al.*, 2024. Ideas and perspectives: Microorganisms in the air through the lenses of atmospheric chemistry and microphysics. *EGUsphere*, 2024, 1-18. https://doi.org/10.5194/egusphere-2024-2377-supplement

Estillore A., *et al.*, 2016. Atmospheric chemistry of bioaerosols: Heterogeneous and multiphase reactions with atmospheric oxidants and other trace gases. *Chem. Sci.*, 7, 6604-6616. https://doi.org/10.1039/C6SC02353

Ewaze J.O., *et al.*, 2008. Ethanol physiology in the warehouse-staining fungus, *Baudoinia compniacensis*. *mycological research*, 112 (11), 1373-1380. https://doi.org/10.1016/j.mycres.2008.05.003

Federici E., *et al.*, 2018. Airborne bacteria and persistent organic pollutants associated with an intense Saharan dust event in the Central Mediterranean. *Sci. Tot. Environ*, 645, 401-410. https://doi.org/10.1016/j.scitotenv.2018.07.128

Franco B., *et al.*, 2020. Spaceborne measurements of formic and acetic acids: A global view of the regional sources. *Geophys. Res. Lett.*, 47 (4), e2019GL086239. https://doi.org/10.1029/2019GL086239

Fraser M.P., Lakshmanan K., 2000. Using levoglucosan as a molecular marker for the long-range transport of biomass combustion aerosols. *Environ. Sci. Technol.*, 34 (21), 4560-4564. https://doi.org/10.1021/es991229

Freedman M., *et al.*, 2019. Role of pH in aerosol processes and measurement challenges. *J. Phys. Chem.*, 123, 1275-1284. https://doi.org/10.1021/acs.jpca.8b10676

Fröhlich-Nowoisky J., *et al.*, 2016. Bioaerosols in the Earth system: Climate, health, and ecosystem interactions. *Atmospheric Research*, 182, 346-376. https://doi.org/10.1016/j.atmosres.2016.07.018

Fu T., *et al.*, 2012. Efficacy, efficiency and safety aspects of hydrogen peroxide vapour and aerosolized hydrogen peroxide room disinfection systems. *J. Hosp. Infect.*, 80, 199-205. https://doi.org/10.1016/j.jhin.2011.11.019

Fuentes-Alburquenque S., *et al.*, 2024. A highly homogeneous airborne fungal community around a copper open pit mine reveals the poor contribution made by the local aerosolization of particles. *Microorganisms*, 12 (934). https://doi.org/10.3390/microorganisms12050934

Garner A.L., 2019. Pulsed electric field inactivation of microorganisms: From fundamental biophysics to synergistic treatments. *Appl. Microbiol. Biotechnol.*, 103 (19), 7917-7929. https://doi.org/10.1007/s00253-019-10067-

Gary C., 1999. *La foudre: Histoire des connaissances, nature du phénomène, risques et mesures de protection*, Masson.

Geisseler D., *et al.*, 2010. Pathways of nitrogen utilization by soil microorganisms–a review. *Soil Biol. Biochem.*, 42 (12), 2058-2067. https://doi.org/10.1016/j.soilbio.2010.08.021

Geller A., 1983. Growth of bacteria in inorganic medium at different levels of airborne organic substances. *Appl. Environ. Microbiol.*, 46 (6), 1258-1262. https://doi.org/10.1128/aem.46.6.1258-1262.1983

Ghosh B., *et al*., 2015. Review of bioaerosols in indoor environment with special reference to sampling, analysis and control mechanisms. *Environ. Int.*, 85, 254-272. https://doi.org/10.1016/j.envint.2015.09.018

Gill P., *et al*., 1983. Organic films on atmospheric aerosol particles, fog droplets, cloud droplets, raindrops, and snowflakes. *Rev. Geophys.*, 21 (4), 903-920. https://doi.org/10.1029/RG021i004p00903

Gligorovski S., *et al*., 2015. Environmental implications of hydroxyl radicals (•OH). *Chem. Rev.*, 115, 13051-13092. https://doi.org/10.1021/cr500310

Goff J., *et al*., 2023. Mixed heavy metal stress induces global iron starvation response. *ISME J.*, 17, 382-392. https://doi.org/10.1038/s41396-022-01351-

Goldberg L., *et al*., 1958. The use of a rotating drum for the. study of aerosols over extended periods of time. *Am. J. Hyg.*, 68 (1), 85-93. https://doi.org/10.1093/oxfordjournals.aje.a119954

Gómez M., *et al*., 2020. Long-term measurement of biogenic volatile organic compounds in a rural background area: Contribution to ozone formation. *Atmos. Environ.*, 224, 117315. https://doi.org/10.1016/j.atmosenv.2020.117315

Gonçalves F.L., *et al*., 2012. Effect of bacterial ice nuclei on the frequency and intensity of lightning activity inferred by the BRAMS model. *Atmos. Chem. Phys.*, 12 (13), 5677-5689. https://doi.org/10.5194/acp-12-5677-2012

Gong J., *et al*., 2020. Concentration, viability and size distribution of bacteria in atmospheric bioaerosols under different types of pollution. *Environmental Pollution*, 257, 113485. https://doi.org/10.1016/j.envpol.2019.113485

Gong Z., *et al*., 2019. Chemical reactions of single optically trapped bioaerosols in a controlled environment. *Aerosol Sci. Technol.*, 53 (8), 853-859. https://doi.org/10.1080/02786826.2019.1621984

Goodsell D.S., 2001. The molecular perspective: Ultraviolet light and pyrimidine dimers. *Stem Cells*, 19 (4), 348-349. https://doi.org/10.1634/stemcells.19-4-348

Goto Y., *et al*., 1990. Acid-induced folding of proteins. *Proc. Natl Acad. Sci. USA,* 87 (2), 573-577. https://doi.org/10.1073/pnas.87.2.573

Graham B., *et al*., 2002. Water-soluble organic compounds in biomass burning aerosols over Amazonia 1. Characterization by NMR and GC-MS. *J. Geophys. Res.: Atmospheres*, 107 (D20), LBA 14-11-LBA 14-16. https://doi.org/10.1029/2001JD000336

Graham W.F., Duce R.A., 1982. The atmospheric transport of phosphorus to the western North Atlantic. *Atmos. Environ.*, 16 (5), 1089-1097. https://doi.org/10.1016/0004-6981(82)90198-

Grahl T., Märkl H., 1996. Killing of microorganisms by pulsed electric fields. *Appl. Microbiol. Biotechnol.*, 45 (1-2), 148-157. https://doi.org/10.1007/s002530050663

Grosjean E., *et al*., 1998. Ambient concentrations of ethanol and methyl tert-butyl ether in Porto Alegre, Brazil, March 1996– April 1997. *Environ. Sci. Technol.*, 32 (6), 736-742. https://doi.org/10.1021/es970788

Gu M., *et al*., 2022. Is fertilization the dominant source of ammonia in the urban atmosphere? *Sci. Tot. Environ*, 838, 155890. https://doi.org/10.1016/j.scitotenv.2022.155890

Guan N., Liu L., 2020. Microbial response to acid stress: Mechanisms and applications. *Appl. Microbiol. Biotechnol.*, 104, 51-65. https://doi.org/10.1007/s00253-019-10226-

Guo H., *et al*., 2006. Regional and local contributions to ambient non-methane volatile organic compounds at a polluted rural/coastal site in Pearl River Delta, China. *Atmos. Environ.*, 40 (13), 2345-2359. https://doi.org/10.1016/j.atmosenv.2005.12.011

Guo L., *et al*., 2021. Systematic review of the effects of environmental factors on virus inactivation: Implications for coronavirus disease 2019. *Int. J. Environ. Sci. Technol.*, 18 (9), 2865-2878. https://doi.org/10.1007/s13762-021-03495-9

Gusbeth C., *et al*., 2024. Bacterial decontamination of process liquids and paints in E-coating lines by pulsed electric field treatment. *Journal of Coatings Technology and Research*, 1-14.

Haddrell A., Thomas R., 2017. Aerobiology: Experimental considerations, observations, and future tools. *Appl. Environ. Microbiol.*, 83 (17), e00809-00817. https://doi.org/10.1128/AEM.00809-17

Haddrell A., *et al*., 2023. Differences in airborne stability of SARS-CoV-2 variants of concern is impacted by alkalinity of surrogates of respiratory aerosol. *J. R. Soc. Interface*, 20 (203), 20230062. https://doi.org/10.1098/rsif.2023.0062

Haddrell A., *et al*., 2024. Ambient carbon dioxide concentration correlates with SARS-CoV-2 aerostability and infection risk. *Nat. Comm.*, 15, 3487. https://doi.org/10.1038/s41467-024-47777-

Haenel F., *et al*., 2015. Reassessment of MIPAS age of air trends and variability. *Atmos. Chem. Phys.*, 15 (22), 13161-13176. https://doi.org/10.5194/acp-15-13161-2015

Hanson R.S., Hanson T.E., 1996. Methanotrophic bacteria. *Microbiol. Rev.*, 60 (2), 439-471. https://doi.org/10.1128/mr.60.2.439-471.1996

Harper G.J., 1961. Airborne micro-organisms: Survival tests with four viruses. *Epidemiol. Infect.*, 59 (4), 479-486. https://doi.org/10.1017/S0022172400039176

Hasegawa N., *et al*., 2011. A study of bacterial culturability during bioaerosol challenge test using a test chamber. *J. Aerosol Sci.*, 42 (6), 397-407. https://doi.org/10.1016/j.jaerosci.2011.02.009

Heesch E.J.M.V., *et al*., 2000. A fast pulsed power source applied to treatment of conducting liquids and air. *IEEE transactions on plasma science*, 28 (1), 137-143. https://doi.org/10.1109/27.842885

Heitkämper T., *et al*., 2024. Flying microbes—survival in the extreme conditions of the stratosphere during a stratospheric balloon flight experiment. *Microbiology Spectrum*, 12 (8), e03982-03923. https://doi.org/10.1128/spectrum.03982-23

Henckel T., *et al*., 2000. Effects of O_2 and CH_4 on presence and activity of the indigenous methanotrophic community in rice field soil. *Environ. Microbiol.*, 2 (6), 666-679. https://doi.org/10.1046/j.1462-2920.2000.00149

Hernandez M., 1999. A combined fluorochrome method for quantitation of metabolically active and inactive airborne bacteria. *Aerosol Sci. Technol.*, 30 (2), 145-160. https://doi.org/10.1080/027868299304741

Hiwar W., *et al*., 2021. What is the relationship between indoor air quality parameters and airborne microorganisms in hospital environments? A systematic review and meta-analysis. *Indoor Air*, 31 (5), 1308-1322. https://doi.org/10.1111/ina.12846

Hong J.-K., *et al*., 2024. The impact of bioaerosol trajectories on microbial community assembly and physicochemical dynamics in the atmosphere. *Sci. Tot. Environ.*, 930, 172736. https://doi.org/10.1016/j.scitotenv.2024.172736

Hůnová I., *et al*., 2023. Ambient ozone at a rural Central European site and its vertical concentration gradient close to the ground. *Environ. Sci. Pollut. Res. Int.*, 30, 80014-80028. https://doi.org/10.1007/s11356-023-28016-

Huynh E., *et al*., 2022. Evidence for a semisolid phase state of aerosols and droplets relevant to the airborne and surface survival of pathogens. *Proc. Natl Acad. Sci. USA,* 119 (4), e2109750119. https://doi.org/10.1073/pnas.2109750119

Ing B., *et al*., 2018. The fungus that likes Scotch whisky. *Field mycology*, 19 (4), 136-140. https://doi.org/10.1016/j.fldmyc.2018.10.007

Ingram L.O., 1989. Ethanol tolerance in bacteria. *Crit. Rev. Biotechnol.*, 9 (4), 305-319. https://doi.org/10.3109/07388558909036741

Irakulis-Loitxate I., *et al*., 2022. Satellites detect abatable super-emissions in one of the world's largest methane hotspot regions. *Environ. Sci. Technol.*, 56 (4), 2143-2152. https://doi.org/10.1021/acs.est.1c04873

Irwin C.K., *et al*., 2011. Using the systematic review methodology to evaluate factors that influence the persistence of influenza virus in environmental matrices. *Appl. Environ. Microbiol.*, 77 (3), 1049-1060. https://doi.org/10.1128/AEM.02733-09

Jacob D.J., *et al*., 2022. Quantifying methane emissions from the global scale down to point sources using satellite observations of atmospheric methane. *Atmos. Chem. Phys.*, 22 (14), 9617-9646. https://doi.org/10.5194/acp-22-9617-2022

Jagger J., 1985. *Solar-UV actions on living cells*, Praeger Publisher, New York, NY (USA).

Jangra R., *et al*., 2023. Efficient deactivation of aerosolized pathogens using a dielectric barrier discharge based cold-plasma detergent in environment device for good indoor air quality. *Sci. Rep.*, 13, 10295. https://doi.org/10.1038/s41598-023-37014-

Karydis V., *et al*., 2021. How alkaline compounds control atmospheric aerosol particle acidity. *Atmos. Chem. Phys.*, 21, 14983-15001. https://doi.org/10.5194/acp-21-14983-2021

Kellogg C.A., *et al*., 2004. Characterization of aerosolized bacteria and fungi from desert dust events in Mali, West Africa. *Aerobiologia*, 20, 99-110. https://doi.org/10.1023/B:AERO.0000032947.88335.bb

Kesavan J.S., Sagripanti J.-L., 2013. Disinfection of airborne organisms by ultraviolet-C radiation and sunlight. *Aerosol Sci.*, 417-439. https://doi.org/10.1002/9781118682555.ch17

Khare P., *et al*., 1999. Atmospheric formic and acetic acids: An overview. *Rev. Geophys.*, 37 (2), 227-248. https://doi.org/10.1029/1998RG900005

Khodadad C.L., *et al*., 2017. Stratosphere conditions inactivate bacterial endospores from a Mars spacecraft assembly facility. *Astrobiology*, 17 (4), 337-350. https://doi.org/10.1089/ast.2016.1549

Kinahan S., *et al*., 2019. Changes of fluorescence spectra and viability from aging aerosolized E. coli cells under various laboratory-controlled conditions in an advanced rotating drum. *Aerosol Sci. Technol.*, 53 (11), 1261-1276. https://doi.org/10.1080/02786826.2019.1653446

King B., *et al*., 2011. Germicidal UV sensitivity of bacteria in aerosols and on contaminated surfaces. *Aerosol Sci. Technol.*, 45 (5), 645-653. https://doi.org/10.1080/02786826.2010.550959

Kirschke S., *et al*., 2013. Three decades of global methane sources and sinks. *Nature geoscience*, 6 (10), 813-823. https://doi.org/10.1038/ngeo1955

Kirstine W.V., Galbally I., 2012. The global atmospheric budget of ethanol revisited. *Atmos. Chem. Phys.*, 12 (1), 545-555. https://doi.org/10.5194/acp-12-545-2012

Klein A.M., *et al*., 2016. Molecular evidence for metabolically active bacteria in the atmosphere. *Front. Microbiol.*, 7, 772. https://doi.org/10.3389/fmicb.2016.00772

Knief C., Dunfield P.F., 2005. Response and adaptation of different methanotrophic bacteria to low methane mixing ratios. *Environ. Microbiol.*, 7 (9), 1307-1317. https://doi.org/10.1111/j.1462-2920.2005.00814

Ko G., *et al*., 2000. Influence of relative humidity on particle size and UV sensitivity of Serratia marcescens and Mycobacterium bovis BCG aerosols. *Tub. Lung Dis.*, 80 (4), 217-228. https://doi.org/10.1054/tuld.2000.0249

Ko G., *et al*., 2002. The characterization of upper-room ultraviolet germicidal irradiation in inactivating airborne microorganisms. *Environ. Health Perspect.*, 110 (1), 95-101. https://doi.org/10.1289/ehp.0211095

Kobayashi F., *et al*., 2015. Bioprocess of Kosa bioaerosols: Effect of ultraviolet radiation on airborne bacteria within Kosa (Asian dust). *J. Biosci. Bioeng.*, 119 (5), 570-579. https://doi.org/10.1016/j.jbiosc.2014.10.015

Kobziar L.N., *et al*., 2022. Wildland fire smoke alters the composition, diversity, and potential atmospheric function of microbial life in the aerobiome. *ISME Communications*, 2 (1). https://doi.org/10.1038/s43705-022-00089-

Kompatscher K., *et al*., 2023. Scoping review on the efficacy of filter and germicidal technologies for capture and inactivation of micro-organisms and viruses. *J. Hosp. Infect.*, 142, 39-48. https://doi.org/10.1016/j.jhin.2023.08.026

Koppmann R., 2020. Chemistry of volatile organic compounds in the atmosphere. *Hydrocarbons, Oils and Lipids: Diversity, Origin, Chemistry and Fate*, 811-822. https://doi.org/10.1007/978-3-319-90569-3_24

Kowalski W., 2010. *Ultraviolet Germicidal Irradiation Handbook: UVGI for Air and Surface Disinfection*, Springer science & business media. https://doi.org/10.1007/978-3-642-01999-9

Krumins V., *et al*., 2008. Retention of inactivated bioaerosols and ethene in a rotating bioreactor constructed for bioaerosol activity studies. *Clean-Soil Air Water*, 593-600. http://dx.doi.org/10.1002/clen.200800004

Krumins V., *et al*., 2014. Substrate-dependent rRNA production in an airborne bacterium. *Environ. Sci. Technol. Letters*, 1 (9), 376-381. https://doi.org/10.1021/ez500245

Kuypers M.M., *et al*., 2018. The microbial nitrogen-cycling network. *Nat. Rev. Microbiol.*, 16 (5), 263-276. https://doi.org/10.1038/nrmicro.2018

Lan X., *et al*., 2024. Trends in globally-averaged CH_4, N_2O, and SF6 determined from NOAA Global Monitoring Laboratory measurements. Version 2024-08.

Lappan R., *et al*., 2024. The atmosphere: A transport medium or an active microbial ecosystem? *ISME J*., 18 (1), wrae092. https://doi.org/10.1093/ismejo/wrae092

Lay J.J., *et al*., 1998. The influence of pH and ammonia concentration on the methane production in high-solids digestion processes. *Water Environ. Res*., 70 (5), 1075-1082. https://doi.org/10.2175/106143098X123426

Lee S.A., *et al*., 2004. Assessment of electrical charge on airborne microorganisms by a new bioaerosol sampling method. *J. Occup. Environ. Hyg*., 1 (3), 127-138. https://doi.org/10.1080/713774377

Leejeerajumnean A., *et al*., 2000. Effect of ammonia on the growth of Bacillus species and some other bacteria. *Lett. Appl. Microbiol*., 30 (5), 385-389. https://doi.org/10.1046/j.1472-765x.2000.00734

Lelieveld J., Dentener F., 2000. What controls tropospheric ozone? *J. Geophys. Res*., 105 (D3), 3531-3551. https://doi.org/10.1029/1999JD901011

Lewis E., Schwartz S., 2004. Sea salt aerosol production: Mechanisms, methods, measurements, and models. *American Geophysical Union*. https://doi.org/10.1029/GM152

Li M., *et al*., 2023. Spatial homogeneity of pH in aerosol microdroplets. *Chem*, 9, 1036-1046. https://doi.org/10.1016/j.chempr.2023.02.019

Li Y., *et al*., 2024. Nonthermal plasma air disinfection for the inactivation of airborne microorganisms in an experimental chamber and indoor air. *J. Appl. Microbiol*., 135 (4). https://doi.org/10.1093/jambio/lxae078

Lidstrom M.E., 2024. Direct methane removal from air by aerobic methanotrophs. *Cold Spring Harbor Perspectives in Biology*, 16 (7). https://doi.org/10.1101/cshperspect.a041671

Lin C.-Y., Li C.-S., 2002. Control effectiveness of ultraviolet germicidal irradiation on bioaerosols. *Aerosol Sci. Technol*., 36, 474-478. https://doi.org/10.1080/027868202753571296

Lin K., Marr L.C., 2020. Humidity-dependent decay of viruses, but not bacteria, in aerosols and droplets follows disinfection kinetics. *Environ. Sci. Technol*., 54 (2), 1024-1032. https://doi.org/10.1021/acs.est.9b04959

Lin K., *et al*., 2020. Survival of MS2 and Φ6 viruses in droplets as a function of relative humidity, pH, and salt, protein, and surfactant concentrations. *PLoS One*, 15 (12), e0243505. https://doi.org/10.1371/journal.pone.0243505

Lin M., *et al*., 2015. Climate variability modulates western US ozone air quality in spring via deep stratospheric intrusions. *Nat. Comm.*, 6 (1), 7105. https://doi.org/10.1038/ncomms8105

Ling M., *et al*., 2021. Properties relevant to atmospheric dispersal of the ice-nucleation active Pseudomonas syringae strain R10. 79 isolated from rain water. *Aerobiologia*, 37, 225-241. https://doi.org/10.1007/s10453-020-09682-

Liu F., *et al*., 2023. Reactive air disinfection technologies: Principles and applications in bioaerosol removal. *ACS EST Engg*, 3, 602-615. https://doi.org/10.1021/acsestengg.3c00016

Liu F., *et al*., 2017. Atmospheric protein chemistry influenced by anthropogenic air pollutants: Nitration and oligomerization upon exposure to ozone and nitrogen dioxide. *Faraday Discuss*, 200, 413-427. https://doi.org/10.1039/C7FD00005G

Liu H., *et al*., 2020. Airborne microorganisms exacerbate the formation of atmospheric ammonium and sulfate. *Environmental Pollution*, 263, 114293. https://doi.org/10.1016/j.envpol.2020.114293

Logan J., 1985. Tropospheric ozone: Seasonal behavior, trends, and anthropogenic influence. *J. Geophys. Res. Atmos*., 90 (D6), 10463-10482. https://doi.org/10.1029/JD090iD06p10463

Lukas M., *et al*., 2020. Electrostatic interactions control the functionality of bacterial ice nucleators. *J. Am. Chem. Soc*., 142 (15), 6842-6846. https://doi.org/10.1021/jacs.9b13069

Luo B., *et al*., 2022. Expiratory aerosol pH: The overlooked driver of airborne virus inactivation. *Environ. Sci. Technol*., 57, 486-497. https://doi.org/10.1021/acs.est.2c05777

Lysenko S.V., 1980. Resistance of microorganisms of upper layers of the atmosphere to ultraviolet radiation and a high vacuum. *Mikrobiologiia*, 49 (1), 175-177.

Lytle C.D., Sagripanti J.-L., 2005. Predicted inactivation of viruses of relevance to biodefense by solar radiation. *Journal of virology*, 79 (22), 14244-14252. https://doi.org/10.1128/JVI.79.22.14244-14252.2005

Madronich S., *et al*., 2018. Solar UV radiation and microbial life in the atmosphere. *Photochemical & Photobiological Sciences*, 17 (12), 1918-1931. https://doi.org/10.1039/c7pp00407

Mahowald N., *et al*., 2008. Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Global biogeochemical cycles*, 22 (4). https://doi.org/10.1029/2008GB003240

Mainelis G., *et al*., 2005. Design and performance of a single-pass bubbling bioaerosol generator. *Atmos. Environ.*, 39 (19), 3521-3533. https://doi.org/10.1016/j.atmosenv.2005.02.043

Mainelis G., *et al*., 2002. Effect of electrical charges and fields on injury and viability of airborne bacteria. *Biotechnology and Bioengineering*, 79 (2), 229-241. https://doi.org/10.1002/bit.10290

Mainelis G., *et al*., 2001. Electrical charges on airborne microorganisms. *J. Aerosol Sci.*, 32, 1087-1110. https://doi.org/10.1016/S0021-8502(01)00039-

Manisalidis I., *et al*., 2020. Environmental and health impacts of air pollution: A review. *Front Public Health*, 8, 14. https://doi.org/10.3389/fpubh.2020.00014

Mao J., *et al*., 2013. Radical loss in the atmosphere from Cu-Fe redox coupling in aerosols. *Atmos. Chem. Phys.*, 13, 509-519. https://doi.org/10.5194/acp-13-509-2013

Marr L.C., *et al*., 2019. Mechanistic insights into the effect of humidity on airborne influenza virus survival, transmission and incidence. *J. R. Soc. Interface*, 16 (150), 20180298. https://doi.org/10.1098/rsif.2018.0298

Martinez M., *et al*., 2010. Hydroxyl radicals in the tropical troposphere over the Suriname rainforest: Airborne measurements. *Atmos. Chem. Phys.*, 10, 3759-3773. https://doi.org/10.5194/acp-10-3759-2010

Masiol M., *et al*., 2020. Hybrid multiple-site mass closure and source apportionment of $PM_{2.5}$ and aerosol acidity at major cities in the Po Valley. *Sci. Tot. Environ.*, 704, 135287. https://doi.org/10.1016/j.scitotenv.2019.135287

Masson-Delmotte V., *et al*., 2021. Climate change 2021: The physical science basis. contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change, 2 (1), 2391.

Mattes T.E., *et al*., 2005. Physiological and molecular genetic analyses of vinyl chloride and ethene biodegradation in *Nocardioides* sp. strain JS614. *Archives of Microbiology*, 183, 95-106. https://doi.org/10.1007/s00203-004-0749-

Mavroidis I., Ilia M., 2012. Trends of NOx, NO_2 and O_3 concentrations at three different types of air quality monitoring stations in Athens, Greece. *Atmos. Environ.*, 63, 135-147. https://doi.org/10.1016/j.atmosenv.2012.09.030

Mayer B., Madronich S., 2004. Actinic flux and photolysis in water droplets: Mie calculations and geometrical optics limit. *Atmos. Chem. Phys.*, 4 (8), 2241-2250. https://doi.org/10.5194/acp-4-2241-2004

Mayol E., *et al*., 2017. Corrigendum: Resolving the abundance and air-sea fluxes of airborne microorganisms in the North Atlantic Ocean. *Front. Microbiol.*, 8, 1971. https://doi.org/10.3389/fmicb.2017.01971

Mcdevitt J., *et al*., 2010. Role of absolute humidity in the inactivation of influenza viruses on stainless steel surfaces at elevated temperatures. *Appl. Environ. Microbiol.*, 76 (12), 3943-3947. https://doi.org/10.1128/AEM.02674-09

Mcdevitt James J., *et al*., 2012. Aerosol susceptibility of influenza virus to UV-C light. *Appl. Environ. Microbiol.*, 78 (6), 1666-1669. https://doi.org/10.1128/AEM.06960-11

Mcgenity T.J., *et al*., 2018. Microbial cycling of isoprene, the most abundantly produced biological volatile organic compound on Earth. *ISME J.*, 12 (4), 931-941. https://doi.org/10.1038/s41396-018-0072-

Mchugh K., *et al*., 2023. Distribution and long-term trends of tropospheric ozone concentrations in Ireland. *Atmosphere*, 14, 569. https://doi.org/10.3390/atmos14030569

Medeiros P.M., *et al*., 2006. Sugars as source indicators of biogenic organic carbon in aerosols collected above the Howland Experimental Forest, Maine. *Atmos. Environ.*, 40 (9), 1694-1705. https://doi.org/10.1016/j.atmosenv.2005.11.001

Mohr A.J., 2007. Fate and transport of microorganisms in air. *Manual of Environ. Microbiol.*, 961-971. https://doi.org/10.1128/9781555815882.ch76

Mønster J., *et al*., 2019. Methodologies for measuring fugitive methane emissions from landfills–A review. *Waste Management*, 87, 835-859. https://doi.org/10.1016/j.wasman.2018.12.047

Moore R.A., *et al*., 2020. Wildland fire as an atmospheric source of viable microbial aerosols and biological ice nucleating particles. *ISME J.*, 15 (2), 461-472. https://doi.org/10.1038/s41396-020-00788-

Morales J., *et al*., 1996. Determination of the levels of Na, K, Ca, Mg, Fe, Zn and Cu in aerosols of the western Venezuelan savannah region. *Sci. Tot. Environ*, 180 (2), 155-164. https://doi.org/10.1016/0048-9697(95)04941-

Morton S.C., Edwards M., 2005. Reduced phosphorus compounds in the environment. *Crit. Rev. Environ. Sci. Technol.*, 35 (4), 333-364. https://doi.org/10.1080/10643380590944978

Mudd J., *et al*., 1969. Reaction of ozone with amino acids and proteins. *Atmos. Environ.*, 3, 669-682. https://doi.org/10.1016/0004-6981(69)90024-

Nair A.A., Yu F., 2020. Quantification of atmospheric ammonia concentrations: A review of its measurement and modeling. *Atmosphere*, 11 (10), 1092. https://doi.org/10.3390/atmos11101092

Nasuhoglu D., *et al*., 2018. Chemical, microbial and toxicological assessment of wastewater treatment plant effluents during disinfection by ozonation. *Chem. Eng. J.*, 346, 466-476. https://doi.org/10.1016/j.cej.2018.04.037

Nazaroff W.W., Weschler C.J., 2020. Indoor acids and bases. *Indoor Air*, 30 (4), 559-644. https://doi.org/10.1111/ina.12670

Nazaroff W.W., Weschler C.J., 2024. Methanol and ethanol in indoor environments. *Indoor Environments*, 100049. https://doi.org/10.1016/j.indenv.2024.100049

Ng T.W., *et al*., 2018. Influence of membrane fatty acid composition and fluidity on airborne survival of Escherichia coli. *Appl. Microbiol. Biotechnol.*, 102 (7), 3327-3336. https://doi.org/10.1007/s00253-018-8826-

Nguyen D.-H., *et al*., 2022. Tropospheric ozone and NOx: A review of worldwide variation and meteorological influences. *Environmental Technology & Innovation*, 28, 102809. https://doi.org/10.1016/j.eti.2022.102809

Nguyen H.T.-H., *et al*., 2001. Atmospheric alcohols and aldehydes concentrations measured in Osaka, Japan and in Sao Paulo, Brazil. *Atmos. Environ.*, 35 (18), 3075-3083. https://doi.org/10.1016/S1352-2310(01)00136-

Nielsen L., *et al*., 2024. Water uptake of airborne cells of *P. syringae* measured with a hygroscopicity tandem differential mobility analyzer. *Environ. Sci. Technol.*, 58, 43, 19211–19221. https://doi.org/10.1021/acs.est.4c01817

Nies D., 1999. Microbial heavy-metal resistance. *Appl. Microbiol. Biotechnol.*, 51 (6), 730-750. https://doi.org/10.1007/s002530051457

Nieto-Caballero M., *et al*., 2022. Carbohydrate vitrification in aerosolized saliva is associated with the humidity-dependent infectious potential of airborne coronavirus. *PNAS Nexus*, 2 (2). https://doi.org/10.1093/pnasnexus/pgac301

Noda J., *et al*., 2022. Air pollution and airborne infection with mycobacterial bioaerosols: A potential attribution of soot. *Int. J. Environ. Sci. Technol.*, 19 (2), 717-726. https://doi.org/10.1007/s13762-021-03203-

Noda J., *et al*., 2019. Atmospheric dust as a possible survival factor for bioaerosols. *E3S Web Conf.*, 99, 04007. https://doi.org/10.1051/e3sconf/20199904007

Nucci C.A., *et al*., 1988. Analyse du champ électromagnétique dû à une décharge de foudre dans les domaines temporel et fréquentiel, *Annales des télécommunications*, 625-637. https://doi.org/10.1007/BF02995262

Oh Y., *et al*., 2020. Reduced net methane emissions due to microbial methane oxidation in a warmer Arctic. *Nature Climate Change*, 10 (4), 317-321. https://doi.org/10.1038/s41558-020-0734-

Okorn K., *et al*., 2021. Characterizing methane and total non-methane hydrocarbon levels in Los Angeles communities with oil and gas facilities using air quality monitors. *Sci. Tot. Environ*, 777. https://doi.org/10.1016/j.scitotenv.2021.146194

Okure D., *et al*., 2022. Characterization of ambient air quality in selected urban areas in Uganda using low-cost sensing and measurement technologies. *Environ. Sci. Technol.*, 56, 3324-3339. https://doi.org/10.1021/acs.est.1c01443

Olefeldt D., *et al*., 2013. Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. *Global Change Biology*, 19 (2), 589-603. https://doi.org/10.1111/gcb.12071

Oswin H., *et al*., 2023. Oxidative stress contributes to bacterial airborne loss of viability. *Microbiol. Spectr.*, 11 (2). https://doi.org/10.1128/spectrum.03347-22

Oswin H., *et al*., 2024. An assessment of the airborne longevity of group A *Streptococcus*. *Microbiol* , 170 (1). https://doi.org/10.1099/mic.0.001421

Oswin H., *et al*., 2022. The dynamics of SARS-CoV-2 infectivity with changes in aerosol microenvironment. *Proc. Natl Acad. Sci. USA,* 119 (27), e2200109119. https://doi.org/10.1073/pnas.2200109119

Otero-Fernandez M., *et al*., 2024. Inactivation mechanisms of *Escherichia coli* in simulants of respiratory and environmental aerosol droplets. *Atmosphere*, 15, 511. https://doi.org/10.3390/atmos15040511

Pan Y.-L., *et al*., 2021. Atmospheric aging processes of bioaerosols under laboratory-controlled conditions: A review. *J. Aerosol Science*, 155, 105767. https://doi.org/10.1016/j.jaerosci.2021.105767

Pan Y.-L., *et al*., 2014. Effects of ozone and relative humidity on fluorescence spectra of octapeptide bioaerosol particles. *Journal of Quantitative Spectroscopy & Radiative Transfer*, 133, 538-550. https://doi.org/10.1016/j.jqsrt.2013.09.017

Paris E.R., *et al*., 2023. Single-cell analysis in hypersaline brines predicts a water-activity limit of microbial anabolic activity. *Science Advances*, 9 (51), eadj3594. https://doi.org/10.1126/sciadv.adj3594

Peccia J., Hernandez M., 2001. Photoreactivation in airborne *Mycobacterium parafortuitum*. *Appl. Environ. Microbiol.*, 67 (9), 4225-4232. https://doi.org/10.1128/AEM.67.9.4225-4232.2001

Peccia J., *et al*., 2001. Effects of relative humidity on the ultraviolet induced inactivation of airborne bacteria. *Aerosol Science & Technology*, 35 (3), 728-740. https://doi.org/10.1080/02786820152546770

Péguilhan R., *et al*., 2024. Clouds influence the functioning of airborne microorganisms. *EGUsphere*, 2024, 1-27. https://doi.org/10.5194/egusphere-2024-2338-supplement

Phan N.-T., *et al*., 2013. Analysis of ammonia variation in the urban atmosphere. *Atmos. Environ.*, 65, 177-185. https://doi.org/10.1016/j.atmosenv.2012.10.049

Phillips G., *et al*., 1964. Effect of air ions on bacterial aerosols. *Int. J. Biometeorol.*, 8 (1), 27-37. https://doi.org/10.1007/BF02186925

Prather M.J., *et al*., 2012. Reactive greenhouse gas scenarios: Systematic exploration of uncertainties and the role of atmospheric chemistry. *Geophys. Res. Lett.*, 39 (9). https://doi.org/10.1029/2012GL051440

Prehn F., *et al*., 2020. Inactivation of airborne bacteria by plasma treatment and ionic wind for indoor air cleaning. *Plasma Process. Polym.*, 17, e2000027. https://doi.org/10.1002/ppap.202000027

Preston H.E., *et al*., 2023. Capture and inactivation of viral particles from bioaerosols by electrostatic precipitation. *iScience*, 26 (9), 107567. https://doi.org/10.1016/j.isci.2023.107567

Prospero J.M., *et al*., 2005. Interhemispheric transport of viable fungi and bacteria from Africa to the Caribbean with soil dust. *Aerobiologia*, 21, 1-19. https://doi.org/10.1007/s10453-004-5872-

Prussin A.J., *et al*., 2018. Survival of the enveloped virus Phi6 in droplets as a function of relative humidity, absolute humidity, and temperature. *Appl. Environ. Microbiol.*, 84 (12), e00551-00518. https://doi.org/10.1128/AEM.00551-18

Pulschen A.A., *et al*., 2015. UV-resistant yeasts isolated from a high-altitude volcanic area on the Atacama Desert as eukaryotic models for astrobiology. *Microbiologyopen*, 4 (4), 574-588. https://doi.org/10.1002/mbo3.262

Pulschen André A., *et al*., 2018. Survival of extremophilic yeasts in the stratospheric environment during balloon flights and in laboratory simulations. *Appl. Environ. Microbiol.*, 84 (23), e01942-01918. https://doi.org/10.1128/AEM.01942-18

Pye H., *et al*., 2020. The acidity of atmospheric particles and clouds. *Atmos. Chem. Phys.*, 20, 4809-4888. https://doi.org/10.5194/acp-20-4809-2020

Qin N., *et al*., 2020. Longitudinal survey of microbiome associated with particulate matter in a megacity. *Genome biology*, 21 (1), 55. https://doi.org/10.1186/s13059-020-01964-

Radajewski S., *et al*., 2000. Stable-isotope probing as a tool in microbial ecology. *Nature*, 403 (6770), 646-649. https://doi.org/10.1038/35001054

Rajwar M.C., *et al*., 2024. Online observation of light non-methane hydrocarbons (C2–C5) over the central Himalayas: Influence of the Indo-Gangetic Plain region. *Atmospheric Pollution Research*, 15 (5), 102078. https://doi.org/10.1016/j.apr.2024.102078

Rangel D.E.N., *et al*., 2018. Fungal strategies for dealing with environment- and agriculture-induced stresses. *Fungal Biology*, 122 (6), 602-612. https://doi.org/10.1016/j.funbio.2018.02.002

Ratnesar-Shumate S., *et al*., 2015. Fluorescence spectra and biological activity of aerosolized *Bacillus* spores and MS2 bacteriophage exposed to ozone at different relative humidities in a rotating drum. *J. Quant. Spectrosc. Radiat. Transf.*, 153, 13-28. https://doi.org/10.1016/j.jqsrt.2014.10.003

Reche I., *et al.*, 2018. Deposition rates of viruses and bacteria above the atmospheric boundary layer. *ISME J.*, 12 (4), 1154-1162. https://doi.org/10.1038/s41396-017-0042-

Rhew R.C., *et al*., 2017. Ethene, propene, butene and isoprene emissions from a ponderosa pine forest measured by relaxed eddy accumulation. *Atmos. Chem. Phys.*, 17 (21), 13417-13438. https://doi.org/10.5194/acp-17-13417-2017

Rigden J.S., 1996. *Macmillan Encyclopedia of Physics.* Simon & Schuster, New York, 353.

Riley M., *et al*., 2022. Tropospheric ozone measurements at a rural town in New South Wales, Australia. *Atmos. Environ.*, 281, 119143. https://doi.org/10.1016/j.atmosenv.2022.119143

Riley R.L., Kaufman J.E., 1972. Effect of relative humidity on the inactivation of airborne *Serratia marcescens* by ultraviolet radiation. *Applied Microbiology*, 23 (6), 1113-1120. https://doi.org/10.1128/am.23.6.1113-1120.1972

Rodó X., *et al*., 2024. Microbial richness and air chemistry in aerosols above the PBL confirm 2,000-km long-distance transport of potential human pathogens. *Proc. Natl Acad. Sci. USA,* 121 (38), e2404191121. https://doi.org/10.1073/pnas.2404191121

Saar M., Salm J., 2014. Emission rate of charged spores in basidiomycetous fungi and the relaxation time of their electric charges. *Aerobiologia*, 30 (1), 71-89. https://doi.org/10.1007/s10453-013-9310-

Saffary R., *et al*., 2002. Microbial survival of space vacuum and extreme ultraviolet irradiation: Strain isolation and analysis during a rocket flight. *FEMS Microbiol. Lett.*, 215 (1), 163-168. https://doi.org/10.1016/S0378-1097(02)00953-

Sale A.J.H., Hamilton W.A., 1967. Effects of high electric fields on microorganisms: I. Killing of bacteria and yeasts. *Biochimica et Biophysica Acta (BBA) – General Subjects*, 148 (3), 781-788. https://doi.org/10.1016/0304-4165(67)90052-

Samaké A., *et al*., 2019a. Polyols and glucose particulate species as tracers of primary biogenic organic aerosols at 28 French sites. *Atmos. Chem. Phys.*, 19 (5), 3357-3374. https://doi.org/10.5194/acp-19-3357-2019

Samaké A., *et al*., 2019b. Arabitol, mannitol, and glucose as tracers of primary biogenic organic aerosol: The influence of environmental factors on ambient air concentrations and spatial distribution over France. *Atmos. Chem. Phys.*, 19 (16), 11013-11030.

Santarpia J., *et al*., 2020. Laboratory study of bioaerosols: Traditional test systems, modern approaches, and environmental control. *Aerosol Sci. Technol.*, 54 (5), 585-600. https://doi.org/10.1080/02786826.2019.1696452

Santarpia J., *et al*., 2012. Changes in fluorescence spectra of bioaerosols exposed to ozone in a laboratory reaction chamber to simulate atmospheric aging. *Opt Express*, 20 (28), 29867-29881. https://doi.org/10.1364/OE.20.029867

Šantl-Temkiv T., *et al*., 2013. Viable methanotrophic bacteria enriched from air and rain can oxidize methane at cloud-like conditions. *Aerobiologia*, 29, 373-384. https://doi.org/10.1007/s10453-013-9287-

Šantl-Temkiv T., *et al*., 2018. Aeolian dispersal of bacteria in southwest Greenland: Their sources, abundance, diversity and physiological states. *FEMS Microbiol. Ecol.*, 94 (4), fiy031. https://doi.org/10.1093/femsec/fiy031

Šantl-Temkiv T., *et al*., 2022. Microbial ecology of the atmosphere. *FEMS Microbiology Reviews*, 46 (4), fuac009. https://doi.org/10.1093/femsre/fuac009

Sattler B., *et al*., 2001. Bacterial growth in supercooled cloud droplets. *Geophys. Res. Lett.*, 28 (2), 239-242. https://doi.org/10.1029/2000GL011684

Saunois M., *et al*., 2020. The Global methane budget 2000-2017. *Earth System Science Data*, 12 (3), 1561-1623.

Sawada S., Totsuka T., 1986. Natural and anthropogenic sources and fate of atmospheric ethylene. *Atmos. Environ.*, 20 (5), 821-832. https://doi.org/10.1016/0004-6981(86)90266-

Scaramboni C., *et al*., 2015. Total sugars in atmospheric aerosols: An alternative tracer for biomass burning. *Atmos. Environ.*, 100, 185-192. https://doi.org/10.1016/j.atmosenv.2014.11.003

Schlesinger W.H., Hartley A.E., 1992. A global budget for atmospheric NH 3. *Biogeochemistry*, 15, 191-211. https://doi.org/10.1007/BF00002936

Schmider T., *et al*., 2024. Physiological basis for atmospheric methane oxidation and methanotrophic growth on air. *Nat. Comm.*, 15 (1), 4151. https://doi.org/10.1038/s41467-024-48197-

Schultz H.L., *et al*., 2003. Assessment of the worldwide market potential for oxidizing coal mine ventilation air methane. EPA-430-R-03-002, 132.

Schwarz J., *et al*., 2022. Bacterial battle against acidity. *FEMS Microbiol Rev*, 46 (6), fuac037. https://doi.org/10.1093/femsre/fuac037

Seager S., *et al*., 2021. The venusian lower atmosphere haze as a depot for desiccated microbial life: A proposed life cycle for persistence of the venusian aerial biosphere. *Astrobiology*, 21 (10). https://doi.org/10.1089/ast.2020.2244

Sharoni S., *et al*., 2015. Infection of phytoplankton by aerosolized marine viruses. *Proc. Natl Acad. Sci. USA,* 112 (21), 6643-6647. https://doi.org/10.1073/pnas.1423667112

Shen F.X., *et al*., 2013. Negatively and positively charged bacterial aerosol concentration and diversity in natural environments. *Chinese Science Bulletin*, 58 (26), 3169-3176. https://doi.org/10.1007/s11434-013-5852-

Shennan J.L., 2006. Utilisation of C2–C4 gaseous hydrocarbons and isoprene by microorganisms. *Journal of Chemical Technology & Biotechnology: International Research in Process, Environmental & Clean Technology*, 81 (3), 237-256. https://doi.org/10.1002/jctb.1388

Simoneit B.R., *et al*., 1999. Levoglucosan, a tracer for cellulose in biomass burning and atmospheric particles. *Atmos. Environ.*, 33 (2), 173-182. https://doi.org/10.1016/S1352-2310(98)00145-

Simoneit B.R., *et al*., 2004. Sugars dominant water-soluble organic compounds in soils and characterization as tracers in atmospheric particulate matter. *Environ. Sci. Technol.*, 38 (22), 5939-5949. https://doi.org/10.1021/es0403099

Sindelarova K., *et al*., 2022. High-resolution biogenic global emission inventory for the time period 2000-2019 for air quality modelling. *Earth System Science Data*, 14 (1), 251-270. https://doi.org/10.5194/essd-14-251-2022

Singh H.B., *et al*., 1995. High concentrations and photochemical fate of oxygenated hydrocarbons in the global troposphere. *Nature*, 378 (6552), 50-54. https://doi.org/10.1038/378050a

Smidt S., *et al*., 2005. Concentrations of ethene and formaldehyde at a valley and a mountain top site in the Austrian Alps. *Atmos. Environ.*, 39 (22), 4087-4091. https://doi.org/10.1016/j.atmosenv.2005.03.028

Smith D.J., *et al*., 2011. Microbial survival in the stratosphere and implications for global dispersal. *Aerobiologia*, 27 (4), 319-332. https://doi.org/10.1007/s10453-011-9203-

Smith D.J., *et al*., 2013. Intercontinental dispersal of bacteria and archaea by transpacific winds. *Appl. Environ. Microbiol.*, 79 (4), 1134-1139. https://doi.org/10.1128/AEM.03029-12

Smith D.J., *et al*., 2018. Airborne bacteria in earth's lower stratosphere resemble taxa detected in the troposphere: Results from a new NASA aircraft bioaerosol collector (ABC). *Front. Microbiol.*, 9, 1752. https://doi.org/10.3389/fmicb.2018.01752

Snider J.R., Dawson G., 1985. Tropospheric light alcohols, carbonyls, and acetonitrile: Concentrations in the southwestern United States and Henry's law data. *J. Geophys. Res.: Atmospheres*, 90 (D2), 3797-3805. https://doi.org/10.1029/JD090iD02p03797

Sobsey M.D., Meschke J.S., 2003. Virus survival in the environment with special attention to survival in sewage droplets and other environmental media of fecal or respiratory origin. Report for the World Health Organization, Geneva, Switzerland, 70, 19-39.

Son E.K., 2009. *Characterization of bacterial processes in the subsurface and the atmosphere*, Rutgers University-Graduate School-New Brunswick.

Songer J.R., 1967. Influence of relative humidity on the survival of some airborne viruses. *Appl. Microbiol.*, 15 (1), 35-42. https://doi.org/10.1128/am.15.1.35-42.1967

Spicer D.B., 2021. Methods and mechanisms of photonic disinfection. *J. Res. Natl Inst. Stand. Technol.*, 126. https://doi.org/10.6028/jres.126.016

Stevenson A., *et al*., 2017. *Aspergillus penicillioides* differentiation and cell division at 0.585 water activity. *Environ. Microbiol.*, 19 (2), 687-697. https://doi.org/10.1111/1462-2920.13597

Straat P.A., *et al*., 1977. Evidence for incorporation of thymidine into deoxyribonucleic acid in airborne bacterial cells. *Appl. Environ. Microbiol.*, 34 (3), 292-296. https://doi.org/10.1128/aem.34.3.292-296.1977

Swanson J., Jeffers D., 1999. Possible mechanisms by which electric fields from power lines might affect airborne particles harmful to health. *Journal of Radiological Protection*, 19 (3), 213. https://doi.org/10.1088/0952-4746/19/3/202

Tadros C., *et al*., 2018. Chemical characterisation and source identification of atmospheric aerosols in the Snowy Mountains, south-eastern Australia. *Sci. Tot. Environ*, 630, 432-443. https://doi.org/10.1016/j.scitotenv.2018.02.231

Tan J., *et al*., 2016. Chemical characteristics and source of size-fractionated atmospheric particle in haze episode in Beijing. *Atmos. Res.*, 167, 24-33. https://doi.org/10.1016/j.atmosres.2015.06.015

Tang J.W., 2009. The effect of environmental parameters on the survival of airborne infectious agents. *J. R. Soc. Interface*, 6 (6), S737-S746. https://doi.org/10.1098/rsif.2009.0227.focus

Thomas R.J., *et al*., 2011. The cell membrane as a major site of damage during aerosolization of *Escherichia coli*. *Appl. Environ. Microbiol.*, 77 (3), 920-925. https://doi.org/10.1128/AEM.01116-10

Tian H., *et al*., 2023. Global nitrous oxide budget 1980–2020. *Earth System Science Data Discussions*, 2023, 1-98.

Tignat-Perrier R., *et al*., 2020. Microbial ecology of the planetary boundary layer. *Atmosphere*, 11 (12), 1296. https://doi.org/10.3390/atmos11121296

Tilgner A., *et al*., 2021. Acidity and the multiphase chemistry of atmospheric aqueous particles and clouds. *Atmos. Chem. Phys.*, 21, 13483–13536. https://doi.org/10.5194/acp-21-13483-2021

Timoshkin I.V., *et al*., 2012. Bactericidal effect of Corona discharges in atmospheric air. *IEEE transactions on plasma science*, 40 (10), 2322-2333. https://doi.org/10.1109/TPS.2012.2193621

Tong Y., Lighthart B., 1997. Solar radiation is shown to select for pigmented bacteria in the ambient outdoor atmosphere. *Photochem. Photobiol.*, 65 (1), 103-106. https://doi.org/10.1111/j.1751-1097.1997.tb01884

Trček J., *et al*., 2015. Adaptation and tolerance of bacteria against acetic acid. *Appl. Microbiol. Biotechnol.*, 99, 6215-6229. https://doi.org/10.1007/s00253-015-6762-

Tribe H.T., *et al*., 2006. Moulds that should be better known: The wine cellar mould, *Racodium cellare* Persoon. *Mycologist*, 20 (4), 171-175. https://doi.org/10.1016/j.mycol.2006.09.016

Tros M.E., *et al*., 1996. Measurement of minimum substrate concentration (Smin) in a recycling fermentor and its prediction from the kinetic parameters of *Pseudomonas* strain B13 from batch and chemostat cultures. *Appl. Environ. Microbiol.*, 62 (10), 3655-3661. https://doi.org/10.1128/aem.62.10.3655-3661.1996

Trouwborst T., *et al*., 1972. Mechanism of inactivation in aerosols of bacteriophage T1. *J. Gen. Virol.*, 15 (3), 235-242. https://doi.org/10.1099/0022-1317-15-3-235

Truyols-Vives J., *et al*., 2024. Antimicrobial activity of safe concentrations of ozone, hydrogen peroxide, and triethylene glycol in air and surfaces. *Environ. Sci.: Atmos.*, 4, 620-633. https://doi.org/10.1039/D3EA00156

Tseng C.-C., Li C.-S., 2005. Inactivation of virus-containing aerosols by ultraviolet germicidal irradiation. *Aerosol Sci. Technol.*, 39 (12), 1136-1142. https://doi.org/10.1080/02786820500428575

Tsong T.Y., 1991. Electroporation of cell membranes. *Biophysical Journal*, 60, 297-306. https://doi.org/10.1016/S0006-3495(91)82054-

Turgeon N., *et al*., 2016. Resistance of aerosolized bacterial viruses to four germicidal products. *PLoS One*, 11 (12), e0168815. https://doi.org/10.1371/journal.pone.0168815

Urban R.C., *et al*., 2014. Sugar markers in aerosol particles from an agro-industrial region in Brazil. *Atmos. Environ.*, 90, 106-112. https://doi.org/10.1016/j.atmosenv.2014.03.034

Van Ginkel C., De Bont J., 1986. Isolation and characterization of alkene-utilizing *Xanthobacter* spp. *Archives of Microbiology*, 145, 403-407. https://doi.org/10.1007/BF00470879

Van Ginkel C., *et al*., 1987. Oxidation of gaseous and volatile hydrocarbons by selected alkene-utilizing bacteria. *Appl. Environ. Microbiol.*, 53 (12), 2903-2907. https://doi.org/10.1128/aem.53.12.2903-2907.1987

Vargin P.N., *et al*., 2015. Stratosphere-troposphere interactions. *Herald of the Russian Academy of Sciences*, 85 (1), 56-63. https://doi.org/10.1134/S1019331615010074

Vaze N., *et al*., 2010. Inactivation of bacteria in flight by direct exposure to nonthermal plasma. *IEEE*, 38 (11), 3234-3240. https://doi.org/10.1109/TPS.2010.2072788

Vejerano E., Marr L., 2018. Physcio-chemical characteristics of evaporating respiratory fluid droplets. *J. R. Soc. Interface*, 15, 20170939. https://doi.org/10.1098/rsif.2017.0939

Verce M.F., *et al*., 2001. Transition from cometabolic to growth-linked biodegradation of vinyl chloride by a *Pseudomonas* sp. isolated on ethene. *Environ. Sci. Technol.*, 35 (21), 4242-4251. https://doi.org/10.1021/es002064

Vieira-Filho M., *et al*., 2016. Water-soluble ions species of size-resolved aerosols: Implications for the atmospheric acidity in São Paulo megacity, Brazil. *Atmos. Res.*, 181, 2811-2287. https://doi.org/10.1016/j.atmosres.2016.07.006

Wagner P., Kuttler W., 2014. Biogenic and anthropogenic isoprene in the near-surface urban atmosphere—A case study in Essen, Germany. *Sci. Tot. Environ*, 475, 104-115. https://doi.org/10.1016/j.scitotenv.2013.12.026

Walker C.M., Ko G., 2007. Effect of ultraviolet germicidal irradiation on viral aerosols. *Environ. Sci. Technol.*, 41 (15), 5460-5465. https://doi.org/10.1021/es070056

Wallington T., *et al*., 2019. 100 years of progress in gas-phase atmospheric chemistry research. *Meteorol. Monogr.*, 59, 10.11-10.52. https://doi.org/10.1175/AMSMONOGRAPHS-D-18-0008

Walter Anthony K., *et al*., 2024. Upland Yedoma taliks are an unpredicted source of atmospheric methane. *Nat. Comm.*, 15 (1), 6056. https://doi.org/10.1038/s41467-024-50346-

Wang Y., *et al*., 2016. Observation of atmospheric peroxides during Wangdu Campaign 2014 at a rural site in the North China Plain. *Atmos. Chem. Phys.*, 16 (17). https://doi.org/10.5194/acp-16-10985-2016

Wang Y., *et al*., 2020. Temporal dynamics of heavymetal distribution and associatedmicrobial community in ambient aerosols from vanadium smelter. *Sci. Tot. Environ.*, 735, 139360. https://doi.org/10.1016/j.scitotenv.2020.139360

Weaver J.E., *et al*., 2019. Systems and methods for studying microbial processes and communities in landfills. *Understanding terrestrial microbial communities*, 129-150. https://doi.org/10.1007/978-3-030-10777-2_

Wei H., *et al*., 2018. Aerosol microdroplets exhibit a stable pH gradient. *Proc. Natl Acad. Sci. USA,* 115 (28), 7272-7277. https://doi.org/10.1073/pnas.1720488115

Wei K., *et al*., 2014. Charge levels and Gram (+/-) fractions of environmental bacterial aerosols. *J. Aerosol Sci.*, 74, 52-62. https://doi.org/10.1016/j.jaerosci.2014.04.002

Wells W.F., 1935. Air-borne infection and sanitary air control. *Journal of Industrial Hygiene*, 17, 253-257.

Whisler B., 1940. The efficacy of ultra-violet light sources in killing bacteria suspended in air. *Iowa State Coll. J. Sci.*, 14, 215-231.

Willey J.D., *et al*., 2019. Rapidly increasing ethanol concentrations in rainwater and air. *npj Climate and Atmospheric Science*, 2 (1), 3. https://doi.org/10.1038/s41612-018-0059-

Womack A.M., *et al*., 2010. Biodiversity and biogeography of the atmosphere. *Philos. Trans. R Soc. Lond. B Biol. Sci.*, 365 (1558), 3645-3653. https://doi.org/10.1098/rstb.2010.0283

Woodward-Massey R., *et al*., 2023. Radical chemistry and ozone production at a UK coastal receptor site. *Atmos. Chem. Phys.*, 23, 14393-14424. https://doi.org/10.5194/acp-23-14393-2023

Wright D., *et al*., 1969. Effect of temperature on survival of airborne *Mycoplasma pneumoniae*. *J. Bacteriol.*, 99 (2), 491-495. https://doi.org/10.1128/jb.99.2.491-495.1969

Xia T., *et al*., 2023. Mobile measurements of atmospheric methane at eight large landfills: An assessment of temporal and spatial variability. *Atmosphere*, 14 (6). https://doi.org/10.3390/atmos14060906

Xie C.Q., *et al*., 2011. A novel method for measuring the charge distribution of airborne microbes. *Aerobiologia*, 27 (2), 135-145. https://doi.org/10.1007/s10453-010-9183-

Xu C., *et al*., 2021. The decay of airborne bacteria and fungi in a constant temperature and humidity test chamber. *Environ. Int.*, 157, 106816. https://doi.org/10.1016/j.envint.2021.106816

Xu P., *et al*., 2003. Efficacy of ultraviolet germicidal irradiation of upper-room air in inactivating airborne bacterial spores and mycobacteria in full-scale studies. *Atmos. Environ.*, 37 (3), 405-419. https://doi.org/10.1016/S1352-2310(02)00825-

Xuan X., *et al*., 2020. Partitioning of hydrogen peroxide in gas-liquid and gas-aerosol phases. *Atmos. Chem. Phys.*, 20, 5513-5526. https://doi.org/10.5194/acp-20-5513-2020

Xue Y., Nicholson W.L., 1996. The two major spore DNA repair pathways, nucleotide excision repair and spore photoproduct lyase, are sufficient for the resistance of *Bacillus subtilis* spores to artificial UV-C and UV-B but not to solar radiation. *Appl. Environ. Microbiol.*, 62 (7), 2221-2227. https://doi.org/10.1128/aem.62.7.2221-2227.1996

Yang W., Marr L.C., 2012. Mechanisms by which ambient humidity may affect viruses in aerosols. *Appl. Environ. Microbiol.*, 78 (19), 6781-6788. https://doi.org/10.1128/AEM.01658-12

Yao M., Mainelis G., 2006. Utilization of natural electrical charges on airborne microorganisms for their collection by electrostatic means. *J. Aerosol Sci.*, 37 (4), 513-527. https://doi.org/10.1016/j.jaerosci.2005.05.006

Yao M., *et al*., 2005. Inactivation of microorganisms using electrostatic fields. *Environ. Sci. Technol.*, 39 (9), 3338-3344. https://doi.org/10.1021/es048808

Ye C., *et al*., 2021. Atmospheric hydrogen peroxide (H_2O_2) at the foot and summit of Mt. Tai: Variations, sources and sinks, and implications for ozone formation chemistry. *J. Geophys. Res. Atmos.*, 126, e2020JD033975. https://doi.org/10.1029/2020JD033975

Yoo H., *et al*., 2024. Direct observation of particle-to-particle variability in ambient aerosol pH using a novel analytical approach based on surface-enhanced Raman spectroscopy. *Environ. Sci. Technol.*, 58, 7977-7985. https://doi.org/10.1021/acs.est.4c00220

Zaitsev I.O., Kuchanskyy V.V., 2021. Corona discharge problem in extra high voltage transmission line. *In*: *Systems, Decision and Control in Energy II* (Zaporozhets A., Artemchuk V., eds), Springer International Publishing, Cham, 3-30. https://doi.org/10.1007/978-3-030-69189-9_

Zeppenfeld S., *et al*., 2021. Aerosol marine primary carbohydrates and atmospheric transformation in the Western Antarctic Peninsula. *ACS Earth and Space Chemistry*, 5 (5), 1032-1047. https://doi.org/10.1021/acsearthspacechem.0c00351

Zhang G., *et al*., 2022. Intercomparison of OH radical measurement in a complex atmosphere in Chengdu, China. *Sci. Tot. Environ*, 838, 155924. https://doi.org/10.1016/j.scitotenv.2022.155924

Zhang L., *et al*., 2016. *Surface charges on aerosol particles–accelerating particle growth rate and atmospheric pollution*. SAGE Publications Sage UK: London, England, 437-440. https://doi.org/10.1177/1420326X16643799

Zhang Y., *et al*., 2024. Impact of haze on potential pathogens in surface bioaerosol in urban environments. *Environ. Pollut.*, 355 (355), 124164. https://doi.org/10.1016/j.envpol.2024.124164

Zhang Y., *et al*., 2020. Isoprene mixing ratios measured at twenty sites in China during 2012–2014: Comparison with model simulation. *J. Geophys. Res.: Atmospheres*, 125 (24), e2020JD033523. https://doi.org/10.1029/2020JD033523

Zhao J., *et al*., 2022. Global airborne bacterial community—interactions with Earth's microbiomes and anthropogenic activities. *Proc. Natl Acad. Sci. USA,* 119 (42), e2204465119. https://doi.org/10.1073/pnas.2204465119

Zhen H., *et al*., 2014. A systematic comparison of four bioaerosol generators: Affect on culturability and membrane integrity when aerosolizing *E. coli* bacteria. *J. Aerosol Sci.*, 70 (4), 67-79. https://doi.org/10.1016/j.jaerosci.2014.01.002

Zuo Z., *et al*., 2013. Association of airborne virus infectivity and survivability with its carrier particle size. *Aerosol Sci. Technol.*, 47 (4), 373-382. https://doi.org/10.1080/02786826.2012.754841

Chapter 6

Metabolic activity of airborne microorganisms

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The conditions to which microbial cells are exposed during aerial transport are probably among the harshest that cells may have to endure during their lifecycle, as described in detail in Chapter 5. The rapid variations of temperature and water and nutrient availability, along with elevated exposure to oxidants and UV, expose microbial cells to multiple shocks and stresses that can have selective impacts on their survival. Microbes are not merely passive travelers in face of these stresses. They exhibit some extent of metabolic activity as responses to them. The taxa that can respond, and their associated biological functions, have been partially described to date. In some cases, microbial responses go beyond mere survival, contributing to atmospheric processes. This include chemical and physical mechanisms that govern atmospheric chemistry, hydrological cycles, and the potential for large-scale dissemination and colonization of new habitats. Clouds and fog in particular, by offering liquid water and dissolved nutrients, could be environments in the atmosphere where significant biological processes occur. This chapter summarizes the current understanding of microbial activity in the atmosphere and the potential implications for biogeochemical and ecological processes.

⏩ Viability, a proxy for metabolic activity

Metabolic activity and viability in microorganisms are intimately connected and often difficult to disentangle. With the exclusion of viruses, for which their viability is still in debate as they are not capable of thriving on their own, both terms can have multiple definitions. For microorganisms such as Bacteria, Archaea and Eukaryotes, viability refers to a potential to multiply under favorable conditions, which implies cell integrity and the maintenance of chemical gradients between intracellular and extracellular spaces. In contrast, metabolic activity relates to the processes actually occurring at the molecular level, and their extent in terms of transfer of energy and/or matter. This involves the processing of substrates, the production of metabolites, the presence of actively transferring electrons in membranes, or again of short-lived bioactive compounds (therefore indicative of recent or on-going metabolic activity) directly responsible for metabolic processes (enzymes, cofactors), and their precursors and regulators (e.g., RNA). Methods intended to detect, quantify and characterize viable microorganisms in environmental samples are summarized elsewhere

(Emerson *et al.*, 2017) and can also be gleaned from the multitude of studies to assess microbial reaction to atmospheric conditions presented in Chapter 5. Depending on their rate, metabolic processes are compatible with cell growth, maintenance, or only survival (dormancy, with repair of cellular damage) (Price and Sowers, 2004).

Detecting, characterizing and quantifying microbial metabolic activity *in situ* in the natural environment is particularly challenging. In the case of the atmosphere, sampling requires at best accumulating material over extended periods of time (e.g., minutes to days) on filters, liquids or other media using active sampling methods to overcome the low biomass. Such processing is likely to alter the actual situation of airborne microorganisms, by causing mortality or inducing changes in their metabolic functioning. This decouples the observations from the situation in the natural environment so that only a potential function is actually often examined. Hence, sampling into a fixative agent appears as a method of choice to examine qualitative aspects of the metabolic functioning of airborne cells such as gene expression patterns (metatranscriptomics, e.g., Amato *et al.*, 2019; Péguilhan *et al.*, 2025).

Methods based on fluorescence can detect molecules linked with metabolic activity (NADH) and quantify bioaerosols online (*i.e.* in real-time), but quantifying microbial activity in terms of element fluxes still requires the incubation of samples. Enzymatic activity measurements typically involve a short-term incubation (ranging from 1 to 1.5 hours) in a liquid medium enriched with an excess of the appropriate substrate. Consequently, they provide only an estimate of the potential enzymatic activity, rather than a quantitative measurement of *in situ* conditions. Finally, biologically-driven reactions can occur outside of cells, through extracellular enzymes in particular, and in damaged cells. There is a (short) period of time in cell's life where metabolic activity occurs without actual viability, as a moribund entity. This has to be kept in mind when considering the activity of microorganisms during their aerial transport, a process that lasts for a few hours to a few days in their lifetime and during which they are likely to lose viability.

Figure 6.1 depicts indicators and drivers of metabolic activity in airborne cells. The detection of ATP (adenosine triphosphate, the "molecular unit of currency" for biochemical energy transfers within cells) in atmospheric samples indicates the presence of viable, and therefore potentially active cells (Amato *et al.*, 2007b; Park *et al.*, 2015; Seshadri *et al.*, 2009). Significant levels of intracellular ATP can be detected at altitudes extending up to the stratosphere (Bryan *et al.*, 2014, 2019; Vaïtilingom *et al.*, 2010).

Typically less than 1% of total bacteria and ~10% of total fungi can be recovered by culture from atmospheric samples (Vaïtilingom *et al.*, 2012). Cultures do not extensively capture viable microorganisms, but they provide clear evidence for viability. Many of the microbial isolates from atmospheric samples are considered generalists and have a high metabolic flexibility, which could contribute to their survival in the atmosphere and more largely to their evolutionary success (Chen *et al.*, 2021b; Sriswasdi *et al.*, 2017). Typical isolates include heterotrophic bacteria affiliated to Pseudomonadota (*Pseudomonas*, *Sphingomonas*, *Methylobacterium*), Actinomycetota (*Streptomyces*, *Rhodococcus*, *Arthrobacter*), and Bacillota (*Bacillus*), along with fungi affiliated to Basidiomycota (*Dioszegia*, *Udeniomyces*, *Cryptococcus*) and Ascomycota (*Tetracladium*, *Aspergillus*, *Fusarium*) (e.g., Adhikari *et al.*, 2004; Charpentier *et al.*, 2024; Fahlgren *et al.*, 2010;

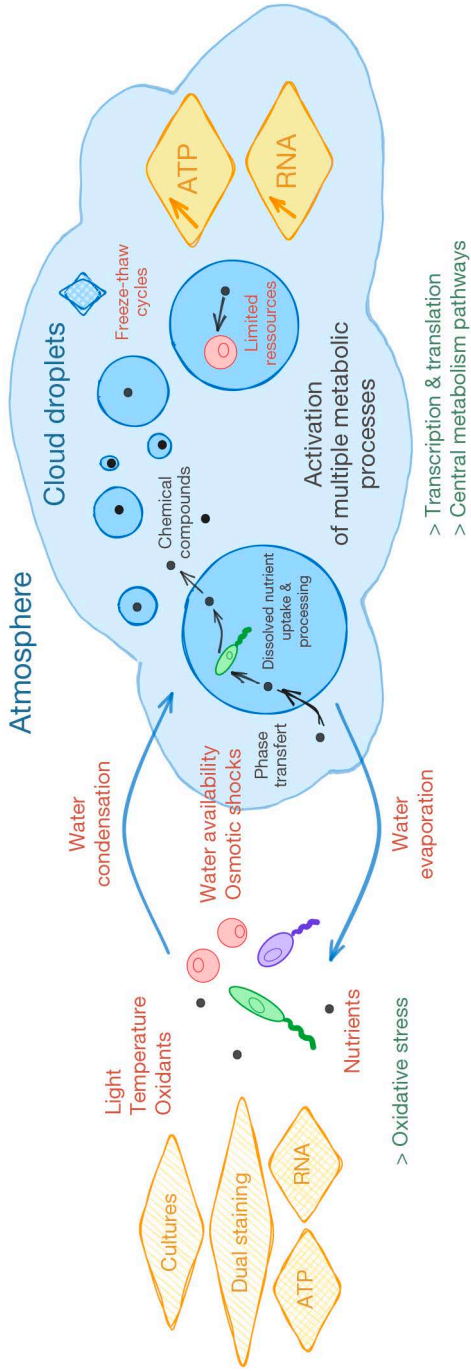

Figure 6.1. Schematic representation of indicators (in yellow) and limiting factors or drivers (in red) of metabolic activity in airborne microbial cells, highlighting the importance of clouds, and main biological functions observed in metatranscriptomes (in green).

Sarmiento-Vizcaíno *et al.*, 2018; Vaïtilingom *et al.*, 2012). Culturable microorganisms also include phototrophic organisms such as algae and cyanobacteria (Dillon *et al.*, 2020). Culturing provided model strains for laboratory studies intended to examine their metabolic capacity to respond to low temperatures (Jousse *et al.*, 2018) and elevated oxidant levels (Wirgot *et al.*, 2019), or their ability to utilize carbon compounds abundant in the atmosphere as substrates (Amato *et al.*, 2007a).

In aerosol chambers, *Sphingomonas aerolata* was shown to elevate ribosome numbers in the presence of biodegradable volatile organic compounds (ethanol and acetic acid) (Krumins *et al.*, 2014), which illustrates the capacity of airborne cells to sense and respond to atmospheric conditions. In natural aerosols, a range of enzymatic activities were detected and quantified, including esterase, proteases, alkaline phosphatase, lipases, and β-glucosidase (Chen *et al.*, 2021a; Malfatti *et al.*, 2019; Wang *et al.*, 2020; Xu *et al.*, 2017; Zhang *et al.*, 2019). These categories of enzymes are involved in multiple metabolic pathways and their presence indicates a potential for biochemical reactions in airborne cells. Esterases notably catalyze the hydrolysis of ester bonds and lead to the release of assimilable organic compounds. These are widely used as general indicators of microbial activity in environmental samples (Adam and Duncan, 2001). Although this is not supported by data, the quantification of esterase activity in atmospheric samples has also been suggested as a potential biomarker of air pollution (Chen *et al.*, 2021a; Zhang *et al.*, 2019).

Culture-independent methods based on cell integrity or functionality of the respiratory chain indicate higher proportions of viable bacteria in aerosols than cultural approaches, with for instance 16% to 91% viable microorganisms at low altitude (*i.e.* around 20 meter above the ground) (Hara and Zhang, 2012; Hill *et al.*, 2007; Hu *et al.*, 2017; Murata and Zhang, 2016), and 2.8% to 6.6% at a mid-altitude mountain site in the free troposphere (Šantl-Temkiv *et al.*, 2017). As the viable –and therefore potentially metabolically active– microbial cells represent only a fraction of the total airborne biodiversity, the affiliation of active microorganisms cannot be adequately inferred from DNA-based data alone. Transcriptomics (RNA-based) provide deeper insights. For instance, in the air above the Amazon forest canopy, fungi mainly consist of Basidiomycota, but the numbers of ribosomes (rRNA), relative to their respective genes, reveal that the active fraction is essentially composed of Ascomycota (Womack *et al.*, 2015). In airborne bacteria as well, ribosome numbers can greatly vary depending on taxa, by 7 orders of magnitude from ~0.001 to ~10,000, with rare taxa being often important members of the active fraction (Amato *et al.*, 2017; Klein *et al.*, 2016; Šantl-Temkiv *et al.*, 2018). Over Greenland, active taxa included Rubrobacteridae and Clostridiales (Šantl-Temkiv *et al.*, 2018), whereas Pseudomonadota affiliated to Alpha- (Sphingomonadales, Rhodospirillales and Rhizobiales), Beta- (Burkholderiales) and Gamma-Proteobacteria (Pseudomonadales) dominated in mid-altitude clouds in France (Amato *et al.*, 2017).

Therefore, depending on the geographic area, the active part of the airborne microbial community can be quantitatively and taxonomically variable due to meteorological conditions (relative humidity, temperature, etc.) and especially due to local emission sources (vegetation, etc.). This may raise several questions and hypotheses regarding ongoing climate change, with the spatial reorganization of ecosystems and vegetation cover on a global scale, as well as the melting of ice and permafrost in polar regions, potentially releasing new viable microorganisms previously trapped in the ice (Ezhova *et al.*, 2021).

Aerial transport is a selective process

For the bacterium *Pseudomonas syringae* in an aerosol, a half-life of ~4 hours was determined in a simulation chamber, indicating that statistically 1 out of ~1 million aerosolized cells survive aerial transport (Amato *et al.*, 2015). Airborne microorganisms outdoor have to cope with multiple adverse conditions, including rapid shifts in humidity and temperature, and exposure to high levels of oxidants, solar and UV irradiation. These can shape the diversity of airborne microorganisms, although the highly multifactorial and strain-dependent aspects of microbial survival in the atmosphere make it difficult to specifically assess and generalize this impact. For instance solar radiation can be a selective pressure for bacteria for physiological traits such as the presence of pigments (Tong and Lighthart, 1997a, 1997b). High humidity favors the survival of *P. syringae* (Marthi *et al.*, 1990), while *Mycoplasma pneumoniae* and *Pasteurella tularensis* survive better at extreme high and low humidity (Wright *et al.*, 1969). Low temperatures are linked with increased survival in *Serratia marcescens*, *Escherichia coli* and *P. syringae*, but these have no influence on survival of the spore forming *Bacillus subtilis* (Ehrlich *et al.*, 1970; Marthi *et al.*, 1990; Wright *et al.*, 1969). The latter can resist stratospheric temperatures, desiccation, and pressure for up to several days, but UV irradiation decimates it within 6 h (Smith *et al.*, 2011). In aqueous suspension, the survival of *Sphingomonas* sp. is particularly affected by osmotic shocks, whereas repeated freeze-thaw cycles impact *Arthrobacter* sp. and *Pseudomonas* spp. populations (Joly *et al.*, 2015). The viability and activity of microbial cells in the atmosphere therefore appear highly variable in space and time, and depend on both cell phenotype and atmospheric conditions (Amato *et al.*, 2023).

Clouds are hotspots of microbial activity in the atmosphere

Water availability is a great limitation for metabolic activity (Stevenson *et al.*, 2015). It is noteworthy that all the aforementioned enzymatic reactions depend on water acting as a nucleophilic agent, so these likely were occurring only in the presence of condensed water. Fog and clouds have attracted most research about microbial activity in the atmosphere so far and based our current knowledge. These environments occupy ~15% of the atmospheric volume (Lelieveld and Crutzen, 1990) and they have strong impacts on atmospheric chemical processes and the composition of the atmosphere (Ervens, 2015; Herrmann *et al.*, 2015).

Data suggest very similar microbial biomass and diversity in clouds as in dry aerosols, with ~10^3 cells/m^3 of air (Péguilhan *et al.*, 2023), and viable fractions ranging from 72% to 95% (Bauer *et al.*, 2002; Hill *et al.*, 2007). Nevertheless, higher ATP-to-cell ratios in clouds compared to precipitation, which include aerosols scavenged from the air column (Péguilhan *et al.*, 2021), along with higher RNA-to-DNA ratio compared with the dry atmosphere (Péguilhan *et al.*, 2025), point to clouds as relative hotspots of microbial activity in the atmosphere. The cellular ATP level is comparable to that in sea or stream water (Hodson *et al.*, 1981; McKnight *et al.*, 1993), and recent data indicate similar potential enzymatic activity as in freshwater systems at the individual cell level (Labed-Veydert *et al.*, in prep.). These findings position clouds as potential key environments for microbial-mediated processes within the vast atmosphere, influencing the transformation of organic and inorganic compounds, with potential cascading effects on the formation of secondary aerosols and cloud dynamics.

Fog in the Pô Valley, Italy, was observed to be associated with higher absolute numbers of airborne culturable bacteria and yeasts than under clear atmospheric conditions (Fuzzi *et al.*, 1997), which led to speculation that atmospheric water could be places where microbial multiplication occurs. Bacteria can indeed significantly develop within a few days in bulk rain or cloud water incubated in laboratory (Amato *et al.*, 2007a; Herlihy *et al.*, 1987), supported by small dissolved organic acids as carbon sources (formate, acetate, succinate, etc.) (Bianco *et al.*, 2019). The high representation of isocitrate lyase transcripts in the metatranscriptomes of clouds, an enzyme that facilitates carbon entry into the glyoxylate cycle, supports the notion that microbial metabolism in natural clouds is oriented toward the utilization of such small organic molecules (Péguilhan *et al.*, 2025). In addition to using small organic compounds in atmospheric water, viable isolates from clouds were also shown to have the capacity to metabolize atmospheric compounds including phenol, formaldehyde, amino acids and others (Amato *et al.*, 2007a; Jaber *et al.*, 2021; Vaïtilingom *et al.*, 2013). Biological activity was also linked with a decrease of oxidant level (H_2O_2) in cloud water, which can have multiple consequences for atmospheric chemistry (Vaïtilingom *et al.*, 2013). Numeric models accounting for the distribution of water among droplets and the heterogeneity of biomass distribution indicate that only semi-volatile and semi-soluble compounds are actually possibly significantly affected by biological processes, due to the necessity of transfer between the gas and the liquid phases (Khaled *et al.*, 2021). Biological processes were estimated to contribute up to 20 ppt and 5 ppt/h (20% and 3%) of the total losses of formic and acetic acids in clouds, respectively (Nuñez López *et al.*, 2024). Under specific conditions, microbial activity in the atmosphere can therefore significantly affect atmospheric composition and the concentrations of volatile organic compounds.

The metabolic signature of microorganisms in clouds, as seen from metatranscriptomics, is distinct from that in non-atmospheric environments, with many transcripts and energy metabolism related in particular to responses to oxidative and osmotic stresses (Amato *et al.*, 2019; Wirgot *et al.*, 2017). The microbial metatranscriptomes in clouds also differ from those under clear atmospheric conditions (Péguilhan *et al.*, 2025). In dry conditions, functions of responses to DNA damage and oxidative stress (SOS response) dominate and indicate greater exposure to stress. In clouds, both prokaryotes and eukaryotes express genes involved in central metabolic pathways, such as the pentose phosphate and tricarboxylic acid cycles. The increased representation in particular of functions related to energy metabolism (ATP production, carbon utilization), metabolic regulations and signaling (MAPK cascade), cytoplasmic translational activity and transmembrane transports of various compounds (e.g., carbohydrates, peptides, ammonium, nitrate) reflect metabolic adjustments and increased overall metabolic activity level, with on-going anabolic processes and increased interactions between cells and their surrounding environment. The metabolic profiles of fungi also strongly suggest that they initiate germination in clouds. This phenomenon is analogous to the "Birch effect" observed in soils, a phenomenon where microbial activity is suddenly triggered by rewetting due to rainfall (Griffiths and Birch, 1961; Unger *et al.*, 2010). In soil, this is associated with the release of gaseous compounds (e.g., N_2O) and it plays important roles in shaping microbial communities. In clouds, such potential gas emissions are necessarily constrained by the low biomass. In addition, despite the favorable conditions of water availability, abundant microbial transcripts related to

responses to glucose and amino acid starvation, autophagy processes and the pentose phosphate pathway reflect an environment where nutrients are scarce and/or difficult to access. While bulk cloud water contains sufficient nutrients to sustain microbial multiplication, this is likely not the case in natural clouds. There, water is distributed among droplets of small volume (on the order of 10^{-6} µL for 20 µm diameter droplets), which greatly limits the access to dissolved compounds. Statistically, there are 10,000 more droplets than microbial cells, indicating that by far most droplets are abiotic, and the biomass is thus concentrated in a very low fraction of them, at high concentration (~10^9 cells/mL in biotic droplets).

By quantifying the biological uptake of radiolabeled precursors of catabolic processes in bulk cloud water (^{3}H-thymidine for nucleic acids and ^{14}C-leucine for proteins), Sattler *et al.* (2001) determined that the microbial biomass production rate at 0°C, a realistic temperature for clouds, was about 0.51 ngC/L/h on average, a value compatible with growth (Price and Sowers, 2004), and corresponding to a cell generation time of about 11 days. This is thus much longer than the estimated lifetime of cloud droplets or the residence time of bacteria in the atmosphere, estimated at around 3.5 days (Burrows *et al.*, 2009), suggesting that significant microbial proliferation during aerial transport is unlikely (Ervens and Amato, 2020). Still, this pointed to the atmosphere as an environment where biological processes may occur, with clouds acting as potential (temporary) microbial habitats for certain taxa. By comparing the diversity of bacteria under clear atmospheric conditions and in clouds, few taxa were found relatively enriched during cloudy conditions (Péguilhan *et al.*, 2023). Only the increased prevalence of *Kocuria* in clouds could be explained by the presence of condensed water only, still without significantly affecting the total biomass. In turn, selective taxa or trait exclusion processes caused by clouds are more likely. Microbial cells have an estimated residence time in the atmosphere of a few days (Burrows *et al.*, 2009) and can undergo 10-11 water evaporation-condensation cycles before being redeposited (Pruppacher and Jaenicke, 1995). Similarly as in soils where dry-wet cycles select for the most responsive microbes (Leizeaga *et al.*, 2022), the repeated osmotic shocks that cells endure during aerial transport could contribute to shaping airborne microbial assemblages toward the most responsive taxa, such as Pseudomonadota and Actinomycetota, which are actually often dominating viable microorganisms in atmospheric samples. These include numerous generalists with great metabolic flexibility and high potential for colonization (Zhou *et al.,* 2016; Chen *et al*., 2021b). In addition, in soils the lag-time before microorganisms re-establish after rewetting shortens with repeated drying-rewetting cycles due to selection processes. While clouds may last several hours, droplets can evaporate within just a few minutes (Dagan *et al.*, 2018; Feingold *et al.*, 1996), so microbial assemblages circulating in the air could progressively acclimate to cloud cycles, and overall respond more readily to water condensation events. Over time, these selective pressures may have driven the evolution of bacterial taxa with enhanced fitness, enabling them to thrive under transient atmospheric conditions and potentially outcompete other species when colonizing new habitats.

Functions and genes beneficial to the microorganisms in their common habitat, such as resistances to antibiotics, could provide crossed selective advantage during aerial transport, by supporting stress responses even in the absence of such molecules, like *qepA*, a plasmid-mediated efflux pump that confers resistance to ciprofloxacin and linked to enhanced tolerance to oxidative stress (Gaurav *et al.*, 2023; Rossi *et al.*,

2023). Mobile genetic elements, including genes involved in heavy metal resistance or metabolic pathways for degrading complex organic compounds, may offer additional adaptive benefits, enabling microbes to better withstand environmental stresses or exploit atmospheric resources. Furthermore, the atmospheric dispersal of microorganisms carrying such genes may facilitate horizontal gene transfer between distant ecosystems, potentially driving the global dissemination of genetic material, including antimicrobial resistance.

⏩ Concluding remarks

While airborne, living microbial cells maintain the capacity to respond to environmental conditions, and potentially acclimate, *i.e.* modulate metabolic functions. However, due to limited residence time allowing at best one cell generation, it is unlikely that they adapt, in the ecological sense, to atmospheric conditions. Still, aerial transport could contribute to microbial evolution through its role as a selective filter to the long-distance dispersal of certain functions and traits.

Looking ahead, climate change is expected to drive a reorganization of the hydrological cycle and atmospheric microbial fluxes. Changes in cloud distribution and altitude, increases in extreme weather events, and prolonged UV exposure are likely to create more spatially and temporally heterogeneous conditions, altering potential microbial habitats while globally elevating stress levels. Together, these dynamics are expected to reshape microbial dispersal, viability, and functional roles in the atmosphere, with probable cascading effects on biogeochemical cycles, ecosystem connectivity, and microbial biodiversity. Addressing these challenges will require a holistic approach, emphasizing the interconnected impacts of microbial activity on environmental, human, and animal health. Such a perspective is essential to better anticipate the far-reaching consequences of atmospheric microbial dynamics in a rapidly changing world.

⏩ Literature cited

Adam G., Duncan H., 2001. Development of a sensitive and rapid method for the measurement of total microbial activity using fluorescein diacetate (FDA) in a range of soils. *Soil Biol. Biochem.*, 33 (7), 943-951. https://doi.org/10.1016/S0038-0717(00)00244-

Adhikari A., *et al.*, 2004. Airborne viable, non-viable, and allergenic fungi in a rural agricultural area of India: A 2-year study at five outdoor sampling stations. *Sci. Tot. Environ*, 326 (1-3), 123-141. https://doi.org/10.1016/j.scitotenv.2003.12.007

Amato P., *et al.*, 2019. Metatranscriptomic exploration of microbial functioning in clouds. *Sci. Rep.*, 9 (1), 4383. https://doi.org/10.1038/s41598-019-41032-

Amato P., *et al.*, 2007a. A fate for organic acids, formaldehyde and methanol in cloud water: Their biotransformation by micro-organisms. *Atmos. Chem. Phys*, 74159-4169. https://doi.org/10.5194/acpd-7-5253-2007

Amato P., *et al.*, 2007b. An important oceanic source of micro-organisms for cloud water at the Puy de Dôme (France). *Atmos. Environ.*, 41 (37), 8253-8263. https://doi.org/10.1016/j.atmosenv.2007.06.022

Amato P., *et al.*, 2017. Active microorganisms thrive among extremely diverse communities in cloud water. *PLoS ONE*, 12 (8), e0182869. https://doi.org/10.1371/journal.pone.0182869

Amato P., *et al.*, 2015. Survival and ice nucleation activity of bacteria as aerosols in a cloud simulation chamber. *Atmos. Chem. Phys.*, 15 (11), 6455-6465. https://doi.org/10.5194/acp-15-6455-2015

Amato P., *et al.*, 2023. The aeromicrobiome: The selective and dynamic outer-layer of the Earth's microbiome. *Front. Microbiol.*, 14, 1186847. https://doi.org/10.3389/fmicb.2023.1186847

Bauer H., *et al.*, 2002. The contribution of bacteria and fungal spores to the organic carbon content of cloud water, precipitation and aerosols. *Atmospheric Research*, 64 (1-4), 109-119. https://doi.org/10.1016/S0169-8095(02)00084-

Bianco A., *et al.*, 2019. Effect of endogenous microbiota on the molecular composition of cloud water: A study by Fourier-transform ion cyclotron resonance mass spectrometry (FT-ICR MS). *Sci. Rep.*, 9 (1), 7663. https://doi.org/10.1038/s41598-019-44149-

Bryan N.C., *et al.*, 2019. Abundance and survival of microbial aerosols in the troposphere and stratosphere. *ISME J.*, 13 (11), 2789-2799. https://doi.org/10.1038/s41396-019-0474-0

Bryan N.C., *et al.*, 2014. A method for sampling microbial aerosols using high altitude balloons. *Journal of Microbiological Methods*, 107, 161-168. https://doi.org/10.1016/j.mimet.2014.10.007

Burrows S.M., *et al.*, 2009. Bacteria in the global atmosphere – Part 2: Modeling of emissions and transport between different ecosystems. *Atmos. Chem. Phys.*, 9 (23), 9281-9297. https://doi.org/10.5194/acp-9-9281-2009

Charpentier T., *et al.*, 2024. Culturable bacteria in clouds at Réunion, tropical island. *Aerobiologia*, 40, 297-302. https://doi.org/10.1007/s10453-024-09819-9

Chen H., *et al.*, 2021a. The microbial activity in $PM_{2.5}$ in indoor air: As an index of air quality level. *Aerosol and Air Quality Research*, 21 (2), 200101. https://doi.org/10.4209/aaqr.2020.03.0101

Chen Y.-J., *et al.*, 2021b. Metabolic flexibility allows bacterial habitat generalists to become dominant in a frequently disturbed ecosystem. *ISME J.*, 15 (10), 2986-3004. https://doi.org/10.1038/s41396-021-00988-w

Dagan G., *et al.*, 2018. Shallow convective cloud field lifetime as a key factor for evaluating aerosol effects. *IScience*, 10, 192-202. https://doi.org/10.1016/j.isci.2018.11.032

Dillon K.P., *et al.*, 2020. Cyanobacteria and algae in clouds and rain in the area of Puy de Dôme, central France. *Appl. Environ. Microbiol.*, 17, 87 (1), e01850-20. https://doi.org/10.1128/AEM.01850-20.

Ehrlich R., *et al.*, 1970. Relationship between atmospheric temperature and survival of airborne bacteria. *Applied Microbiology*, 19 (2), 245-249. https://doi.org/10.1128/am.19.2.245-249.1970

Emerson J.B., *et al.*, 2017. Schrödinger's microbes: Tools for distinguishing the living from the dead in microbial ecosystems. *Microbiome*, 5 (1), 86. https://doi.org/10.1186/s40168-017-0285-3

Ervens B., 2015. Modeling the processing of aerosol and trace gases in clouds and fogs. *Chemical Reviews*, 115 (10), 4157-4198. https://doi.org/10.1021/cr5005887

Ervens B., Amato P., 2020. The global impact of bacterial processes on carbon mass. *Atmos. Chem. Phys.*, 20 (3), 1777-1794. https://doi.org/10.5194/acp-20-1777-2020

Ezhova E., *et al.*, 2021. Climatic factors influencing the anthrax outbreak of 2016 in Siberia, Russia. *EcoHealth*, 18 (2), 217-228. https://doi.org/10.1007/s10393-021-01549-5

Fahlgren C., *et al.*, 2010. Annual variations in the diversity, viability, and origin of airborne bacteria. *Appl. Environ. Microbiol.*, 76 (9), 3015-3025. https://doi.org/10.1128/AEM.02092-09

Feingold G., *et al.*, 1996. The relationship between drop in-cloud residence time and drizzle production in numerically simulated stratocumulus clouds. *Journal of Atmospheric Sciences*, 53 (8), 1108-1122. https://doi.org/10.1175/1520-0469(1996)053<1108:TRBDIC>2.0.CO;2

Fuzzi S., *et al.*, 1997. Fog droplets—an atmospheric source of secondary biological aerosol particules. *Atmos. Environ.*, 31 (2), 287-290. https://doi.org/10.1016/1352-2310(96)00160-4

Gaurav A., *et al.*, 2023. Role of bacterial efflux pumps in antibiotic resistance, virulence, and strategies to discover novel efflux pump inhibitors. *Microbiology*, 169 (5), 001333. https://doi.org/10.1099/mic.0.001333

Griffiths E., Birch H.F., 1961. Microbiological changes in freshly moistened soil. *Nature*, 189 (4762), 424-424. https://doi.org/10.1038/189424a0

Hara K., Zhang D., 2012. Bacterial abundance and viability in long-range transported dust. *Atmos. Environ.*, 47, 20-25. https://doi.org/10.1016/j.atmosenv.2011.11.050

Herlihy L.J., *et al.*, 1987. Bacterial utilization of formic and acetic acid in rainwater. *Atmos. Environ.*, 21, 2397-2402. https://doi.org/10.1016/0004-6981(87)90374-X

Herrmann H., *et al.*, 2015. Tropospheric aqueous-phase chemistry: Kinetics, mechanisms, and its coupling to a changing gas phase. *Chemical Reviews*, 115 (10), 4259-4334. https://doi.org/10.1021/cr500447k

Hill K.A., *et al.*, 2007. Processing of atmospheric nitrogen by clouds above a forest environment. *J. Geophys. Res.: Atmospheres*, 112 (D11), 2006JD008002. https://doi.org/10.1029/2006JD008002

Hodson R.E., *et al.*, 1981. Dissolved adenosine triphosphate utilization by free-living and attached bacterioplankton. *Marine Biology*, 64 (1), 43-51. https://doi.org/10.1007/BF00394079

Hu W., *et al.*, 2017. Concentration and viability of airborne bacteria over the kuroshio extension region in the northwestern Pacific Ocean: Data from three cruises. *J. Geophys. Res.: Atmospheres*, 122 (23), 12892-12905. https://doi.org/10.1002/2017JD027287

Jaber S., *et al.*, 2021. Biotic and abiotic transformation of amino acids in cloud water: Experimental studies and atmospheric implications. *Biogeosciences*, 18 (3), 1067-1080. https://doi.org/10.5194/bg-18-1067-2021

Joly M., *et al.*, 2015. Survival of microbial isolates from clouds toward simulated atmospheric stress factors. *Atmos. Environ.*, 11792-98. https://doi.org/10.1016/j.atmosenv.2015.07.009

Jousse C., *et al.*, 2018. Metabolomic study of the response to cold shock in a strain of Pseudomonas syringae isolated from cloud water. *Metabolomics*, 14 (1), 11. https://doi.org/10.1007/s11306-017-1295-7

Khaled A., *et al.*, 2021. Biodegradation by bacteria in clouds: An underestimated sink for some organics in the atmospheric multiphase system. *Atmos. Chem. Phys.*, 21 (4), 3123-3141. https://doi.org/10.5194/acp-21-3123-2021

Klein A.M., *et al.*, 2016. Molecular evidence for metabolically active bacteria in the atmosphere. *Front. Microbiol.*, 7, 7, 772. https://doi.org/10.3389/fmicb.2016.00772

Krumins V., *et al.*, 2014. Substrate-dependent rRNA production in an airborne bacterium. *Environ. Sci. Technol. Letters*, 1 (9), 376-381. https://doi.org/10.1021/ez500245y

Leizeaga A., *et al.*, 2022. Repeated drying and rewetting cycles accelerate bacterial growth recovery after rewetting. *Biology and Fertility of Soils*, 58 (4), 365-374. https://doi.org/10.1007/s00374-022-01623-2

Lelieveld J., Crutzen P.J., 1990. Influences of cloud photochemical processes on tropospheric ozone. *Nature*, 343 (6255), 227-233. https://doi.org/10.1038/343227a0

Malfatti F., *et al.*, 2019. Detection of active microbial enzymes in nascent sea spray aerosol: Implications for atmospheric chemistry and climate. *Environ. Sci. Technol. Letters*, 6 (3), 171-177. https://doi.org/10.1021/acs.estlett.8b00699

Marthi B., *et al.*, 1990. Survival of bacteria during aerosolization. *Appl. Environ. Microbiol.*, 56 (11), 3463-3467. https://doi.org/10.1128/aem.56.11.3463-3467.1990

McKnight D.M., *et al.*, 1993. Seasonal relationships between planktonic microorganisms and dissolved organic material in an alpine stream. *Biogeochemistry*, 21 (1), 39-59. https://doi.org/10.1007/BF00002687

Murata K., Zhang D., 2016. Concentration of bacterial aerosols in response to synoptic weather and land-sea breeze at a seaside site downwind of the Asian continent. *J. Geophys. Res.: Atmospheres*, 121 (19), 11636-11647. https://doi.org/10.1002/2016JD025028

Nuñez López L., *et al.*, 2024. Bacteria in clouds biodegrade atmospheric formic and acetic acids. *Atmos. Chem. Phys.*, 24 (9), 5181-5198. https://doi.org/10.5194/acp-24-5181-2024

Park J.-W., *et al.*, 2015. Fast monitoring of indoor bioaerosol concentrations with ATP bioluminescence assay using an electrostatic rod-type sampler. *PLoS ONE*, 10 (5), e0125251. https://doi.org/10.1371/journal.pone.0125251

Péguilhan R., *et al.*, 2021. Rainfalls sprinkle cloud bacterial diversity while scavenging biomass. *FEMS Microbiol. Ecol.*, 97 (11), fiab144. https://doi.org/10.1093/femsec/fiab144.

Péguilhan R., *et al.*, 2023. Comparative analysis of bacterial diversity in clouds and aerosols. *Atmos. Environ.*, 119635. https://doi.org/10.1016/j.atmosenv.2023.119635

Péguilhan R., *et al.*, 2025. Clouds influence the functioning of airborne microorganisms. *Biogeosciences*, 22, 1257-1275. https://doi.org/10.5194/bg-22-1257-2025

Price P.B., Sowers T., 2004. Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proc. Natl Acad. Sci. USA,* 101 (13), 4631-4636. https://doi.org/10.1073/pnas.0400522101

Pruppacher H.R., Jaenicke R., 1995. The processing of water vapor and aerosols by atmospheric clouds, a global estimate. *Atmospheric Research*, 38 (1-4), 283-295. https://doi.org/10.1016/0169-8095(94)00098-X

Rossi F., *et al.*, 2023. Quantification of antibiotic resistance genes (ARGs) in clouds at a mountain site (puy de Dôme, central France). *Sci. Tot. Environ*, 865, 161264. https://doi.org/10.1016/j.scitotenv.2022.161264

Šantl-Temkiv T., *et al.*, 2017. High-flow-rate impinger for the study of concentration, viability, metabolic activity, and ice-nucleation activity of airborne bacteria. *Environ. Sci. Technol.*, 51 (19), 11224-11234. https://doi.org/10.1021/acs.est.7b01480

Šantl-Temkiv T., *et al.*, 2018. Aeolian dispersal of bacteria in southwest Greenland: Their sources, abundance, diversity and physiological states. *FEMS Microbiol. Ecol.*, 94 (4). https://doi.org/10.1093/femsec/fiy031

Sarmiento-Vizcaíno A., *et al.*, 2018. Atmospheric precipitations, hailstone and rainwater, as a novel source of streptomyces producing bioactive natural products. *Front. Microbiol.*, 9, 773. https://doi.org/10.3389/fmicb.2018.00773

Sattler B., *et al.*, 2001. Bacterial growth in supercooled cloud droplets. *Geophys. Res. Lett.*, 28 (2), 239-242. https://doi.org/10.1029/2000GL011684

Seshadri S., *et al.*, 2009. Application of ATP bioluminescence method to characterize performance of bioaerosol sampling devices. *J. Aerosol Sci.*, 40 (2), 113-121. https://doi.org/10.1016/j.jaerosci.2008.10.002

Smith D.J., *et al.*, 2011. Microbial survival in the stratosphere and implications for global dispersal. *Aerobiologia*, 27 (4), 319-332. https://doi.org/10.1007/s10453-011-9203-5

Sriswasdi S., *et al.*, 2017. Generalist species drive microbial dispersion and evolution. *Nat. Comm.*, 8 (1), 1162. https://doi.org/10.1038/s41467-017-01265-1

Stevenson A., *et al.*, 2015. Multiplication of microbes below 0.690 water activity: Implications for terrestrial and extraterrestrial life. *Environ. Microbiol.*, 17 (2), 257-277. https://doi.org/10.1111/1462-2920.12598

Tong Y., Lighthart B., 1997a. Solar radiation has a lethal effect on natural populations of culturable outdoor atmospheric bacteria. *Atmos. Environ.*, 31 (6), 897-900. https://doi.org/10.1016/S1352-2310(96)00235-X

Tong Y., Lighthart B., 1997b. Solar radiation is shown to select for pigmented bacteria in the ambient outdoor atmosphere. *Photochem. Photobiol.*, 65 (1), 103-106. https://doi.org/10.1111/j.1751-1097.1997.tb01884.x

Unger S., *et al.*, 2010. The influence of precipitation pulses on soil respiration – Assessing the "Birch effect" by stable carbon isotopes. *Soil Biol. Biochem.*, 42 (10), 1800-1810. https://doi.org/10.1016/j.soilbio.2010.06.019

Vaïtilingom M., *et al.*, 2010. Contribution of microbial activity to carbon chemistry in clouds. *Appl. Environ. Microbiol.*, 76 (1), 23-29. https://doi.org/10.1128/AEM.01127-09

Vaïtilingom M., *et al.*, 2012. Long-term features of cloud microbiology at the puy de Dôme (France). *Atmos. Environ.*, 56, 88-100. https://doi.org/10.1016/j.atmosenv.2012.03.072

Vaïtilingom M., *et al.*, 2013. Potential impact of microbial activity on the oxidant capacity and organic carbon budget in clouds. *Proc. Natl Acad. Sci. USA,* 110 (2), 559-564. https://doi.org/10.1073/pnas.1205743110

Wang B., *et al.*, 2020. Characteristics of microbial activity in atmospheric aerosols and its relationship to chemical composition of $PM_{2.5}$ in Xi'an, China. *J. Aerosol Sci.*, 146, 105572. https://doi.org/10.1016/j.jaerosci.2020.105572

Wirgot N., *et al.*, 2017. H_2O_2 modulates the energetic metabolism of the cloud microbiome. *Atmos. Chem. Phys.*, 17 (24), 14841-14851. https://doi.org/10.5194/acp-17-14841-2017

Wirgot N., *et al.*, 2019. Metabolic modulations of *Pseudomonas graminis* in response to H_2O_2 in cloud water. *Sci. Rep.*, 9 (1), 1-14. https://doi.org/10.1038/s41598-019-49319-2

Womack A.M., *et al.*, 2015. Characterization of active and total fungal communities in the atmosphere over the Amazon rainforest. *Biogeosciences*, 12 (21), 6337-6349. https://doi.org/10.5194/bg-12-6337-2015

Wright D.N., *et al.*, 1969. Effect of temperature on survival of airborne *Mycoplasma pneumoniae*. *Journal of Bacteriology*, 99 (2), 491-495. https://doi.org/10.1128/jb.99.2.491-495.1969

Xu A., *et al.*, 2017. Seasonal variability in bacterial and fungal diversity and community composition of the near-surface atmosphere in coastal megacity. *Aerobiologia*, 33 (4), 555-575. https://doi.org 10.1007/s10453-017-9489-z

Zhang S., *et al.*, 2019. Seasonal variation of microbial activity and pathogenic bacteria under non-serious pollution levels in Beijing. *Aerosol and Air Quality Research*, 19 (8), 1798-1807. https://doi.org/10.4209/aaqr.2019.05.0256

Zhou X., *et al.*, 2016. The resilience of microbial community under drying and rewetting cycles of three forest soils. *Front. Microbiol.*, 7. https://doi.org/10.3389/fmicb.2016.01101

Chapter 7

Release of primary biological aerosol particles from surface waters

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Water surfaces represent some of the most significant interfaces in nature for the exchange of biological material with the atmosphere. Water bodies naturally contain a diverse and numerous population of viruses, bacteria, fungal spores, and algae. Their abundance at the surface is enhanced by the presence of a microlayer of biological and organic material that forms at the interface between water and air due to the hydrophobic nature of some organic compounds (Cunliffe *et al.*, 2013). This enriched microlayer becomes particularly important when considering the various mechanisms that can transfer these microorganisms from water to air. The mechanisms of emissions associated with these microlayers are rather distinct from the mechanisms described in the other chapters of this book.

Any mechanism that entraps air into the surface of water is capable of contributing to the emission of microorganisms as aerosols. Throughout this chapter we will use the term aerosolization. This can be accomplished through bubble bursting, such as waterfalls, rainfall, turbulence, and most importantly, waves. Complete or fragmented entities of biological material emitted into the atmosphere are often termed primary biological aerosol particles (PBAPs) (Després *et al.*, 2012). These PBAPs, once airborne, play crucial roles in climate, environmental and health processes (Figure 7.1), as will be discussed throughout this chapter. Most aerolization mechanisms are largely controlled by wind shear, hence wind energy is considered a main contributor to the number of airborne water microorganisms. Salt-rich waters, such as oceans, contribute further by also producing salt aerosol particles to which microorganisms can attach and become more easily airborne (Patterson *et al.*, 2016). While these fundamental mechanisms drive the initial release of PBAPs, their subsequent distribution and behaviour in the environment exhibit much greater complexity.

PBAPs released from surface waters exhibit complex and variable spatial and temporal patterns, which are influenced by various environmental factors, as will be described in the following. The emitted particles exhibit high diversity in size, morphology, biological, and surface compositions that reflect the dynamic nature of the microbiological communities and water properties. PBAPs from surface water can be emitted with other aerosol particles, either as individual particles, agglomerates, or fragments.

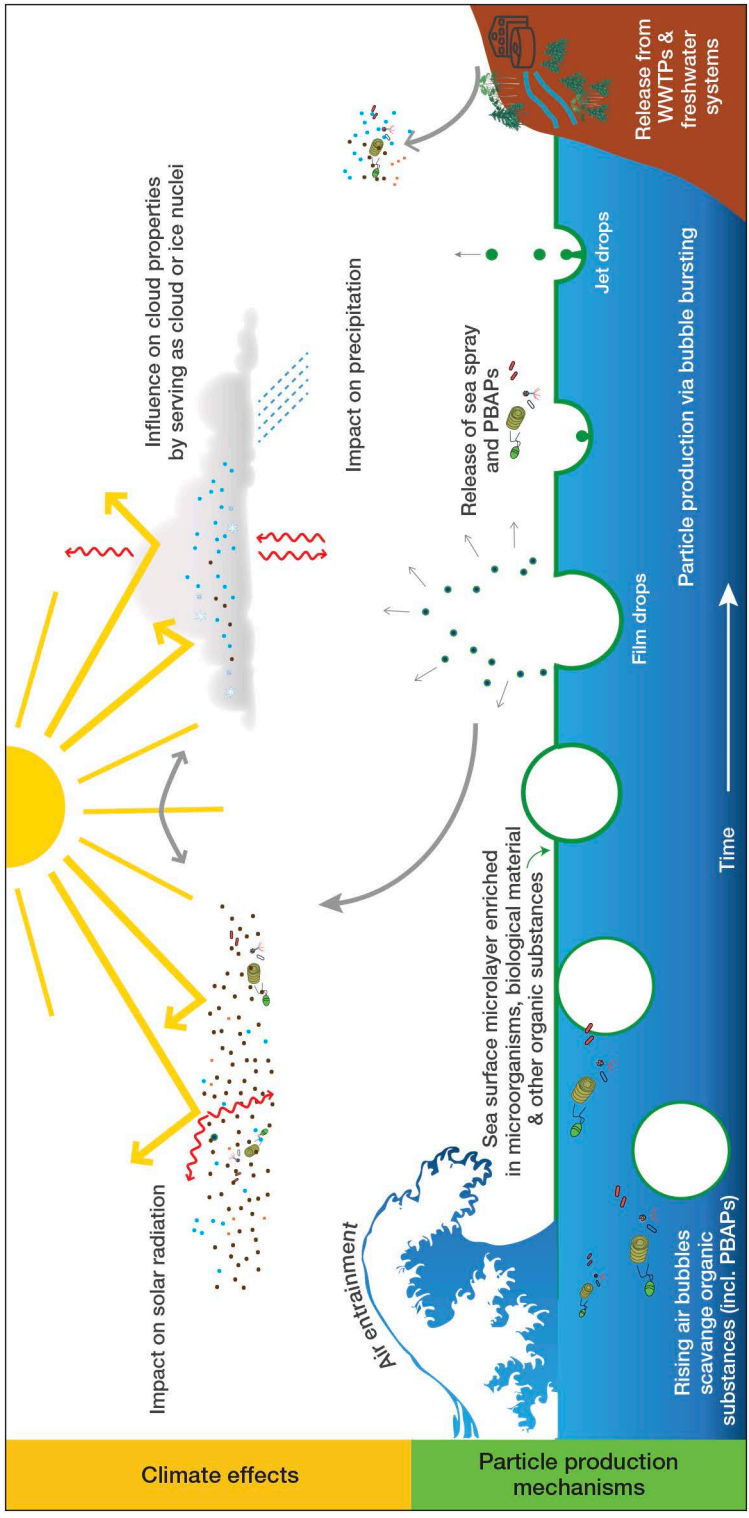

Figure 7.1. Main particle production mechanisms and climatic effects of primary biological aerosol particles (PBAPs) from surface waters.

The main pathway of aerozolisation of PBAPs from surface water is via bubble bursting due to the entrainment of air (e.g., from breaking waves). Once in the atmosphere, PBAPs can interact with solar radiation and influence cloud microphysical properties and consequently precipitation. PBAPs released from waste water treatment plants (WWTPs) or from harmful algal blooms also impact air quality and can have adverse health effects to humans.

The diverse emission behavior further impacts their environmental properties and also complicates their analysis. Spatial distributions are highly heterogeneous, with variations driven by geographic location, water temperature, salinity, and the biogeochemical state of surface water itself (e.g., influence of nutrient levels, proximity to coasts, settlements, etc.). Seasonal dynamics plays a crucial role, with PBAP emissions peaking during periods of high biological activity in surface waters, such as summer algae blooms. Temporal variability is also affected by meteorological conditions such as wind speed and temperature. These conditions influence both aerosolization processes and the diel cycle of organisms in the water, which in turn affects the availability of nutrients at different depths. Once in the air, meteorological conditions further determine not only the transport but also the viability of the PBAPs in the atmosphere as described in Chapters 5 and 6. These complex distribution patterns and survival mechanisms ultimately determine how PBAPs influence both environmental processes and human health.

PBAPs emitted from surface waters have wide-ranging impacts on both climate and human health. In the atmosphere, they can interact with solar radiation or serve as nucleating particles for cloud droplets or ice crystals. In marine environments, PBAPs may be particularly significant, sometimes postulated to be the main source of ice nucleating particles (Burrows *et al.*, 2013; Wilson *et al.*, 2015) and, in turn, likely play an important role in precipitation formation (Huffman *et al.*, 2013). Recent studies have demonstrated that PBAPs are a dominant source of warm-temperature ice nuclei (Freitas *et al.*, 2023; Cornwell *et al.*, 2023), driving overall uncertainties in nuclei prediction and cloud properties in models (Cornwell *et al.*, 2023). From a health perspective, several illnesses are related to exposure to airborne water microorganisms such as Cyanobacteria or Rotaviruses, particularly in areas above oceans, coastal lands, and near wastewater runoff.

Here, we will describe the main characteristics of PBAPs released from surface water based on previous and recent findings. We will discuss the main underlying release mechanisms of PBAPs to the atmosphere and present their main atmospheric transport pathways and environmental impacts. Finally, a short summary of knowledge gaps and research challenges will be presented.

⏩ Release from ocean waters

The study of marine-derived PBAPs and their importance in various climate, ecological and biogeochemical processes is sometimes called *ocean aerobiology* (Alsante *et al.*, 2021). Here, we will summarize the main mechanisms underlying the release of marine PBAP, as well as the main findings from field and laboratory/mesocosm experiments.

Sea spray aerosol formation

In the oceans, the release of PBAPs into the atmosphere is inherently tied to the mechanisms of release of sea spray particles, opposite to terrestrial self-driven emissions such as fungal spores or pollen. Sea spray particles are the largest source of natural aerosol particles on Earth (Seinfeld and Pandis, 2006), where wind-driven breaking waves are considered to be the main catalyzer of sea spray aerosol (SSA) production (Woodcock, 1953). Breaking waves entrain air into the water, creating bubbles

that rise towards the surface. Droplets are injected into the atmosphere when these bubbles burst (see Figure 7.1). Here, two main droplets can be identified: the film and jet droplets (Lewis, 2006). A large number of droplets of mainly sub-micrometer size are formed by bursting the thin bubble cap, the so-called film droplets (Knelman *et al.*, 1954; Spiel, 1998). Film droplets are enriched in hydrophobic matter, cell fragments, and small microorganisms such as bacteria and viruses from the surface microlayer (Wang *et al.*, 2017). The bursting of the bubble cap is followed by the ejection of fewer, so-called jet droplets, which are produced by the collapse of the remaining air bubble cavity. Jet droplets are found mainly in the super-micrometer size range (Lewis, 2006) and consist mainly of sea salt, water-soluble organics, and microorganisms from subsurface waters (Wang *et al.*, 2017). It should be noted that other droplets also exist, such as splash or spume droplets (Andreas *et al.*, 1995), which are, however, of less importance due to their large size and shorter atmospheric residence time. Although sea spray production increases with increasing wind speeds, high wind speeds can prevent the enrichment of microorganisms in the surface microlayer and thus affect PBAP aerosolization (Rahlff *et al.*, 2017; Zinke *et al.*, 2024b). Beyond wind-driven wave breaking, the production of sea spray is influenced by various physicochemical and biological factors of seawater. Among these, temperature and salinity play particularly important roles in both the physical process of spray formation and the biological availability of microorganisms for aerosolization, as we will explore in detail below.

The influence of seawater temperature on the formation of SSA was first identified in laboratory experiments (e.g., Woolf *et al.*, 1987), where it was observed that the production of sea spray particles increased as the water temperature decreased. Subsequent studies in the last 20 years corroborated these findings in greater detail consistently reporting similar trends (Mårtensson *et al.*, 2003; Salter *et al.*, 2014; Nielsen and Bilde, 2020; Zinke *et al.*, 2022; Sofieva *et al.*, 2022). However, it should be noted that some studies have also reported different effects of temperature on particle production (Forestieri *et al.*, 2018; Schwier *et al.*, 2017; Christiansen *et al.*, 2019). The temperature dependence has also been implemented within Earth system models (Salter *et al.*, 2015; Döscher *et al.*, 2022). While these physical effects of temperature on sea spray formation are well documented, temperature also plays a crucial biological role. Seawater temperature directly affects the growth, reproduction, and metabolic rates of marine microorganisms such as bacteria, phytoplankton, and zooplankton (e.g., Price and Sowers, 2004). Warmer temperatures typically enhance microbial metabolic rates and growth, increasing the abundance of bacteria and phytoplankton in seawater and the surface microlayer, and thus their aerosolization potential. Seasonal warming can promote phytoplankton blooms and harmful algal blooms, which enhance the potential to aerosolize harmful biological particles.

In addition to temperature effects, seawater salinity represents another fundamental property that influences sea spray formation, although its effects are less well understood. Laboratory experiments using artificial seawater or sodium chloride solutions have reported mixed results. Several studies have reported an increase in particle production and a shift toward larger modal particle diameters at higher salinities (Mårtensson *et al.*, 2003; Russell and Singh, 2006; Tyree *et al.*, 2007; Zábori *et al.*, 2012; Zinke *et al.*, 2022; Dubitsky *et al.*, 2023), although others did not find such a size shift (Park *et al.*, 2014; May *et al.*, 2016). A common finding is that the flux of SSA production is most sensitive to salinities below 10 g kg^{-1}, likely due to the reduced

coalescence of bubbles, resulting in smaller bubbles in seawater compared to freshwater (Lewis and Schwartz, 2004; Craig *et al.*, 1993). Dubitsky *et al.* (2023) showed that salinity not only affects bubble coalescence but also systematically influences the length scale of the rupturing bubble film.

Beyond these physical effects, changes in salinity also significantly impact the biological aspects of aerosolization. Harb *et al.* (2021) showed a nonmonotonic response of bacteria aerosolization with changing salinity with a maximum at oligohaline conditions, a decline at higher oligohaline conditions, and a moderate increase at polyhaline–euhaline conditions.

To systematically study these various influences on SSA formation, researchers have developed several experimental approaches. The generation of SSA can be achieved in various ways, e.g. by creating bubbles in simulation chambers using a fine-pored diffuser or the so-called "frits" (Mårtensson *et al.*, 2003), by using plunging jets (Tyree *et al.*, 2007; Salter *et al.*, 2014; May *et al.*, 2016) or within wave channels (Sauer *et al.*, 2022). For experiments using frits, the size distribution of the water bubbles produced is highly dependent on the specific pore size of the diffuser, leading to differences in the physical and chemical properties of the produced sea spray (e.g., Zieger *et al.*, 2017). Sea spray simulation chambers using plunging jets have been shown to generate bubble size distributions that are more similar to those produced by breaking waves over the ocean (Hultin *et al.*, 2011). However, while the emission and physical properties of sea or lake spray aerosols are highly influenced by the aerosolization method, the impact of these different approaches on PBAP coemission remains an important open question for future research.

Mesocosm studies

The emission of PBAP from seawater has been studied in controlled environments, both in the laboratory and on board research vessels, using sea spray simulation chambers (Figures 7.2a and 7.2b) or wave channels. These mesocosm experiments allow researchers to study PBAP enrichment, composition, and emission behavior under controlled conditions.

The first mesocosm experiments investigating enrichment factors (EF) in marine aerosol production were conducted by Blanchard and Syzdek (1972), who examined a suspension of *Serratia marcescens* in distilled water to assess the dynamics of EF. The results indicated that initial jet drops exhibited significantly higher EFs, reaching up to 1,200, whereas the final jet drops had much lower values, around 8. Later, Blanchard and Syzdek (1982) reported film drop EFs ranging from 10 to 20. In another study, Cipriano (1979) conducted mesocosm experiments using *S. marinorubra* in seawater taken from the coast of Long Island, finding that film drop EFs varied between 50 and 100.

As research in this field progressed, subsequent mesocosm studies employed culture-based methods to estimate airborne microbial abundance in regions such as the Baltic Sea and the Arctic Ocean (Marks *et al.*, 2001; Hultin *et al.*, 2011; Fahlgren *et al.*, 2015). However, it is important to recognize that culture-based approaches can underestimate the microbial presence, since less than 1% of bacteria are cultivable. Marks *et al.* (2001) analyzed Baltic seawater samples from the Bay of Gdańsk in July 1997

and March 1998, reporting EFs of 37–2,545 for mesophilic bacteria and 14–585 for psychrophilic bacteria. Hultin *et al.* (2011) conducted experiments in the Baltic Sea between May and September 2005 and estimated that total airborne bacterial concentrations are in the range 10^4–10^6 cells m^{-3} (or 10^1–10^3 cells L^{-1}), assuming that all bacteria exhibited transport efficiencies similar to colony forming units (CFU).

In another approach, Aller *et al.* (2005) used inverted funnels and frits to generate SSA from seawater while operating from a floating catamaran deployed in Long Island Sound (June to September 2003). Bacteria were enumerated via fluorescence microscopy using DAPI staining, with reported EFs around 10. However, frits have been observed to create a narrower bubble size distribution compared to natural breaking waves, which may lead to a bias toward smaller bubbles and the preferential ejection of jet drops from subsurface water (Stokes *et al.*, 2013).

Further mesocosm experiments were conducted by Rastelli *et al.* (2017) in the North-Eastern Atlantic (June-July 2006), utilizing a plunging jet sea spray simulation chamber. The abundance of bacteria in aerosol samples, collected with a five-stage Berner impactor, was assessed by epifluorescence microscopy. Their findings indicated size-dependent bacterial enrichment in SSA, with EFs around 45 for particles smaller than 1.2 μm, while enrichment was significantly lower for larger particles. In a different experimental approach, Michaud *et al.* (2018) used wave channel experiments at Scripps Pier (San Diego, USA) and used flow cytometry to determine the abundance of airborne bacterial species, reporting EFs of approximately 11 in SSA compared to bulk seawater.

More recent studies have further advanced our understanding of these processes. Zinke *et al.* (2024b) quantified microbial enrichment in SSAs also from Baltic seawater, with factors ranging from 13 to 488 compared to the underlying seawater, which decreased with increasing plunging jet flow rates. They also demonstrated selective aerosolization of bacteria, which led to a less diverse microbial community in aerosols than in seawater. Finally, Zinke *et al.* (2024a) conducted mesocosm experiments in the North-eastern Atlantic, where the microbial enrichment factors in SSA ranged between 9 and 158. The study emphasized selective aerosolization processes and reported reduced microbial diversity in aerosols compared to seawater, influenced by seawater microbial dynamics and selective bacterial growth.

The methodological approaches among these studies vary significantly. Notably, Rastelli *et al.* (2017) and Zinke *et al.* (2024a, 2024b) introduced an important advancement by normalizing their EF calculations using sodium concentrations. This normalization is crucial, as mesocosm-based estimates of microbial or PBAP emissions can be influenced by several factors, including seawater biogeochemistry (e.g., salinity, temperature, surfactants) and experimental conditions (e.g., bubble production methods, bubbling rate, sampling port positioning, chamber size, and whether the setup is closed or flow-through). Variability in experimental designs requires caution when comparing results between studies. By adjusting EFs for sodium concentration, variations in SSA emission fluxes can be better accounted for, allowing for more consistent cross-study comparisons. To enhance the accuracy and reliability of microbial enrichment and emission assessments, we strongly recommend normalizing the EF calculations using relevant ionic markers such as sodium. A summary with a comparison of airborne microbial concentrations and EF based on the work by Zinke *et al.* (2024a) is given in Table 7.1.

Recent advances in real-time single-particle analysis instruments utilizing ultraviolet light-induced fluorescence enable the continuous monitoring of fluorescent PBAP. For example, using a multiparameter bioaerosol spectrometer (Ruske *et al.*, 2017), Freitas *et al.* (2022) investigated PBAP emissions from Baltic seawater, identifying that approximately 1 in 10,000 particles larger than 0.8 µm were fluorescent PBAPs. Their study highlighted significant morphological transitions in particles influenced by seawater biogeochemistry. In addition, Freitas *et al.* (2022) observed preferential emission of specific bacterial taxa in aerosols, distinct from the seawater community (Figure 7.2c), similar to what has been observed by Fahlgren *et al.* (2015).

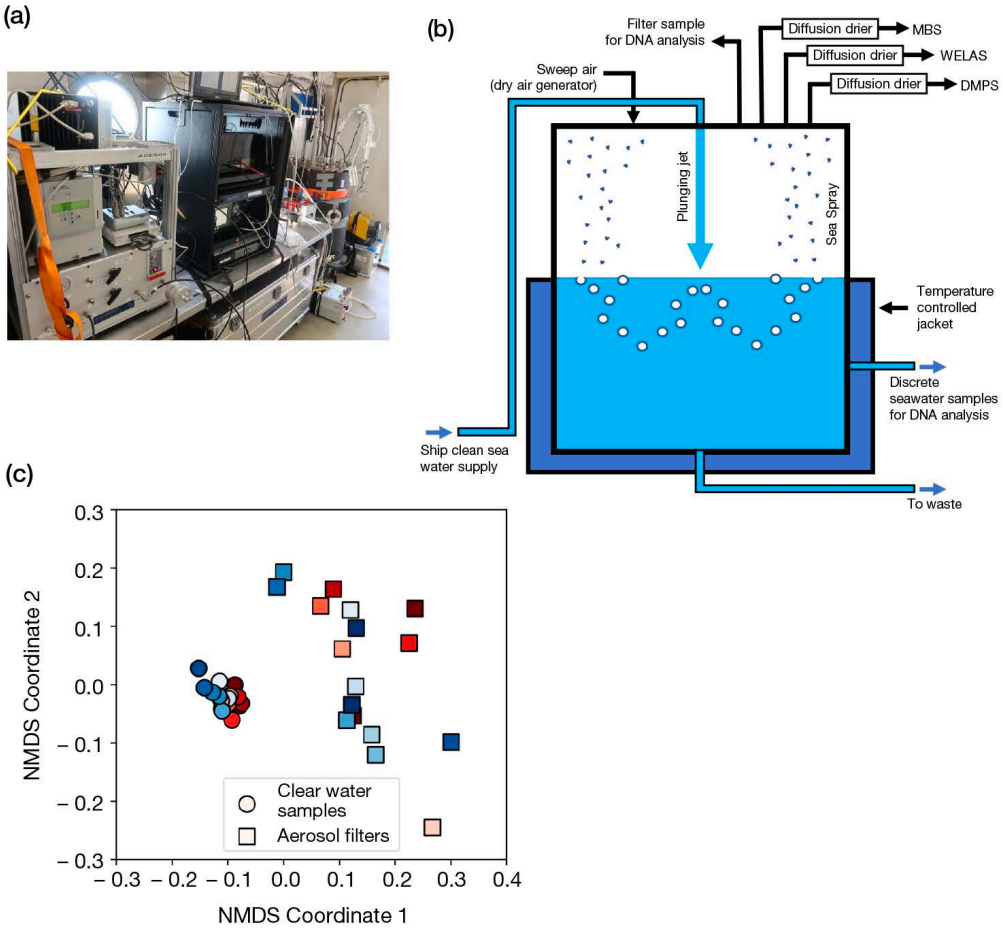

Figure 7.2. Example of a mesocosm experiment by Freitas *et al.* (2022) studying the release of PBAPs from Baltic seawater.

(**a**) Set-up on board the R/V *Elisabeth Mann Borgese* with the sea water intake on the left, aerosol *in situ* instruments in the middle and the sea spray simulation chamber on the right of the photo. (**b**) Schematic of the set-up, where sea water is continuously added via the plunging jet to the chamber which is flushed in the headspace with particle-free air. Sampling of bioaerosols is done using various offline and online sampling techniques. (**c**) Result of the non-metric multidimensional scaling (NMDS) analysis of the aerosol and chamber water samples showing the preferential aerosolization of bioaerosols.

Table 7.1. Comparison of airborne microbial concentrations and enrichment factors across various mesocosm experiments.

Study	Source of seawater	Microbial concentration (/m^3)	Enrichment factor (EF)	Experimental set-up
Blanchard and Syzdek (1972)	*S. marcescens* suspension	ND	1,200* (first jet drop) 8* (last jet drop)	Glass beaker (V = 0.4 L) and frit, CFU enumeration on gelatin filters
Blanchard and Syzdek (1982)	*S. marcescens* suspension	ND	10-20* (film drops, D = 1.7 mm)	Drops produced by nozzle, electrostatic precipitation on gelatin-coated glass slides for CFU enumeration
Cipriano and Blanchard (1981)	*S. marinorubra* suspension	ND	50-100* (film drops, D = 10 µm)	Plunging sheet chamber (V = 35 L) + Andersen sampler, CFU enumeration on culture medium
Marks *et al.* (2001)	Baltic Sea (Bay of Gdańsk)	1–100 CFU (mesophilic bacteria) 1–100 CFU (psychrophilic bacteria)	37-2,545* 14-585*	Chamber (V = 5 L) and frit, CFU enumeration on gelatin filters
Aller *et al.* (2005)	Long Island (New York)	$1–8{\cdot}10^4$	10*	Inverted funnels and frit on a floating catamaran, enumeration with FM
Hultin *et al.* (2011)	Baltic Sea	$10^2–10^4$ CFU $10^4 – 10^6$ total microbes	-	Plunging jet chambers in recirculating mode (V = 50 L) and flow-through mode (V = 20 L), total microbe enumeration with FM, CFU enumeration on gelatin filters
Fahlgren *et al.* (2015)	Arctic Ocean	$0.2–2{\cdot}10^3$ CFU	-	Recirculating plunging jet chamber (V = 180 L), CFU enumerations on gelatin filters
Rastelli *et al.* (2017)	North-Eastern Atlantic (close to Ireland)	$0.1–2.1{\cdot}10^5$	45 (for D_p < 1.2 µm)	Plunging jet chamber, enumeration with FM
Michaud *et al.* (2018)	North-Eastern Pacific (Scripps Pier)	$1–6{\cdot}10^7$	11*	Wave channel (V = 13,000 L), enumeration with FC
Zinke *et al.* (2024a)	North-Eastern Atlantic (Azores archipelago)	$1{\cdot}10^4–1.7{\cdot}10^5$ mean $5.3{\cdot}10^4 \pm 5.0{\cdot}10^4$	9.1-158 mean 48.6 ± 35.6	Recirculating plunging jet chamber (V = 25 L), enumeration with FM
Zinke *et al.* (2024b)	Baltic Sea	$1.8{\cdot}10^5 \pm 4.6{\cdot}10^4$ at 1.3 L/min flow rate $2.4{\cdot}10^51 \pm 7.8{\cdot}10^4$ at 2.6 L/min flow rate	13-488 mean 262.6 ± 162.4 at 1.3 L/min 47.0 ± 36.2 at 2.6 L/min	Plunging jet chamber (V = 90 L) at flow rates 1.3 and 2.6 L/min, enumeration with FM

*not normalized to sodium. CFU, colony forming units; FM, fluorescence microscopy; FC, flow cytometry; *V,* volume; *D,* diameter; ND, no data. Adapted from Zinke *et al.* (2024a).

While these real-time analysis methods have provided new insights, parallel advances in traditional culture-based methods, particularly the transition to next-generation sequencing, have further deepened our understanding of airborne bacterial communities. These advances have revealed that certain water-dwelling microbial taxa are selectively aerosolized, particularly those with hydrophobic surface properties that facilitate their transfer to the sea surface microlayer and subsequent incorporation into SSA (Fahlgren *et al.*, 2015; Rastelli *et al.*, 2017; Perrott *et al.*, 2017; Michaud *et al.*, 2018; Freitas *et al.*, 2022; Zinke *et al.*, 2024a, 2024b). This selective aerosolization process, combined with regional variations in microbial populations, leads to distinct airborne microbial communities across different marine environments, as demonstrated in studies spanning the Atlantic and Pacific Oceans, and the North and Baltic Seas (Seifried *et al.*, 2015; Michaud *et al.*, 2018; Mayol *et al.*, 2017; Lang-Yona *et al.*, 2022).

⏩ Release from freshwater systems

Freshwater ecosystems, including lakes, rivers, and reservoirs, are significant sources of bioaerosols, though they remain understudied compared to marine systems due to their limited surface coverage and high variability. While these aerosols originate from similar biological and physical processes as marine systems, with emissions primarily driven by wind and turbulence, their impact tends to be concentrated in the local environment rather than having broader geographical reach.

The local significance of freshwater bioaerosols has become increasingly apparent through recent studies highlighting their potential health and environmental risks, particularly in connection with harmful algal blooms (May *et al.*, 2018). For example, Olson *et al.* (2020) demonstrated that aerosolized particles generated from Mona Lake in the U.S. contained cyanobacterial toxins, including mycocystins that pose potential inhalation risks to human populations living near affected water bodies. The importance of understanding these risks is growing, as the frequency of harmful algal blooms is expected to increase in a warming climate (e.g., Paerl and Huisman, 2009), warranting further research on the specific mechanisms of release and their quantification.

⏩ Release from waste water treatment plants

Wastewater treatment plants (WWTPs) can be a source of bioaerosols that pose significant health risks to WWTP workers and nearby communities. Untreated wastewater contains a diverse range of microorganisms, including viruses, bacteria, and fungi, which can also include pathogenic entities (Gerardi and Zimmerman, 2004; Korzeniewska, 2011). Once in the air, these microorganisms can be inhaled, ingested, or deposited on surfaces, posing significant risks to human health and affecting air quality (Tian *et al.*, 2022). Bioaerosol aerosolization can occur in various steps of wastewater treatment, such as in the aeration process, in the filtering steps, or in other mixing steps by bursting waste water and foam bubbles (Gerardi and Zimmerman, 2004). Recently, it was shown that bacteria originating from WWTPs in a coastal and highly populated site were returning to land as SSA (Pendergraft *et al.*, 2023), highlighting the importance of better understanding the health effects of aerosols, including PBAPs, emitted or re-emitted from WWTPs.

Understanding these health implications requires consideration of the complex dynamics of sources, aerosolization, dispersal, exposure, and health effects of PBAPs from WWTPs (Tian *et al.*, 2022). For example, the transport or dispersal and viability of the biological particles released are highly dependent on the meteorological conditions (especially the speed of the wind, the intensity of the Sun and the relative humidity) at the site (Korzeniewska, 2011). Substantial knowledge gaps remain regarding human health exposure and risk from WWTP bioaerosols, hampering the development of effective risk assessment and management strategies.

Although the literature on WWTP bioaerosol emissions is limited, recent reviews by Tian *et al.* (2022) and Korzeniewska (2011) provide a comprehensive overview of both findings and methodological approaches. These reviews evaluate two main categories of sampling and analysis methods: offline and online techniques. Offline bioaerosol sampling employs standard aerosol sampling techniques, ranging from impactor, cyclone impinger, or filter sampling, with subsequent laboratory analysis using either culture- or non-culture-based approaches (e.g., DNA/RNA sequencing techniques). Although these methods are highly sensitive for determining the composition and concentration of microbiological communities, they generally suffer from low time resolution and low repeatability. Online techniques, developed more recently, are based on single-particle fluorescence, shape, and size measurements (Tian *et al.*, 2020). These methods enable the study of fast and dynamic processes at high time resolution around all parts of WWTPs. However, they can potentially underestimate or overcount bioaerosols due to limitations in their size range covered and the applied fluorescence technique (Pöhlker *et al.*, 2012; Zinke *et al.*, 2024a). Given these methodological limitations, Tian *et al.* (2022) emphasize the importance of using parallel complementary methods and conducting dedicated laboratory studies for better instrument characterization in future research.

⏩ Transport pathways

Most global-scale climate models exclude bioaerosols due to a limited understanding of their emission mechanisms, atmospheric lifetime, and climate impacts (Burrows *et al.*, 2009; Hoose *et al.*, 2010; Sesartic *et al.*, 2012). While some progress has been made in modeling certain types of bioaerosols, such as annual terrestrial fungal spore emissions (Janssen *et al.*, 2021), global-scale estimates of surface water PBAP emissions remain rare. Initial modeling studies have focused on a fundamental question: whether surface ocean waters acted as sinks or sources of bioaerosols and their transport between ecosystems (Burrows *et al.*, 2009). Their findings suggest that the sea surface is likely a sink, where the deposition rate of microorganisms exceeds that of emission.

To better understand these transport patterns, researchers have turned to direct analysis of air samples. Studies analyzing rRNA genes from air samples over the Pacific and Atlantic Oceans have detected both marine and terrestrial bacteria, with evidence of long-range transport spanning hundreds to thousands of kilometers. However, the relative rates of bacterial deposition and emission remain unclear, and crucial information about the atmospheric lifetime of marine microorganisms and their climatic impacts during transport is lacking. Complementing these open-ocean studies, observational research in coastal regions using microscopy, rRNA,

and fluorescence techniques has recorded inbound transport of marine microorganisms from nearby oceans (Pendergraft *et al.*, 2023). These findings suggest that microorganisms emitted from surface waters play an important role not only in the atmosphere above the oceans but also in nearby coastal regions (Lighthart, 1997), where pathogenic organisms can pose significant risks to coastal communities (Wiśniewska *et al.*, 2022).

⏩ Knowledge gaps, challenges and outlook

Despite significant advances in understanding the emissions of PBAPs from surface water, several knowledge gaps and challenges remain. These challenges span all relevant fields of biology, atmospheric science, and environmental science, including impact and health effects, highlighting the complexity of studying PBAPs at the interface between water and atmosphere. Filling these gaps is important for improving our predictive modeling capabilities and for fully evaluating the impacts of PBAPs on climate, ecosystems, and human health.

One major challenge in studying PBAP emissions from surface waters is the lack of standardized methodologies to measure the PBAPs released in both qualitative and quantitative manner. Currently, a wide range of sampling, collection, and analysis methods have been applied for the identification and quantification of PBAPs between studies, making it difficult to compare results and draw more general conclusions. Advances in optical single-particle techniques or sequencing technologies offer promising pathways to improve PBAP characterization and quantification, but these methods have yet to be widely adopted or standardized for these purposes. Determining the actual flux of PBAPs from surface waters in the ambient atmosphere remains to be determined in various environments (Šantl-Temkiv *et al.*, 2022; Amato *et al.*, 2023). This could, for example, be done using the eddy covariance or eddy relaxation technique. The difficulties of such measurements are described in Chapter 3. These methodological limitations directly impact our ability to characterize PBAP composition and diversity, which have not yet been fully documented at the global or regional level. Although surface water is well established to host a wide variety of microorganisms, there is limited understanding of which taxa are preferentially aerosolized. Inventories of taxonomic information remain incomplete, particularly for marine PBAPs. These may differ significantly from PBAPs released from freshwater systems or WWTPs. More advanced molecular-level-based studies using e.g. genomics or proteomics are only recently being applied in studies around PBAPs. These approaches could provide more detailed information on the biological origins and functional behavior of PBAPs released from surface waters. This could help to link specific organisms or biomolecules to atmospheric processes such as nucleation of ice within clouds (e.g., Pummer *et al.*, 2015; Pandey *et al.*, 2016; Roeters *et al.*, 2021; Lukas *et al.*, 2022; Hartmann *et al.*, 2022).

While these molecular approaches offer promising insights into PBAP composition, understanding how environmental factors influence these patterns presents another significant challenge. Environmental factors such as temperature, salinity, and nutrient availability strongly influence the composition of the microbial community in surface waters, but their effects on PBAP emissions remain poorly understood. In addition, temporal variability is another critical factor which has received limited

attention. For example, seasonal variations in surface waters lead to fluctuations in the type and amount of PBAPs released, but these patterns remain largely not quantified. Furthermore, all environmental factors are expected to change in a warming climate, which will further complicate the predictions of the impact of PBAP on future environments.

Meteorological conditions largely govern the atmospheric dispersal and viability of PBAPs, which, in turn, determines their environmental impact. Like all aerosols, PBAPs undergo *atmospheric aging* –physical, chemical, and biological transformations that alter their properties and environmental fate. Although particle and PBAP aging is known to depend strongly on meteorological conditions, the underlying processes of atmospheric aging and their consequences on the properties and survival of PBAPs in the atmosphere are not fully understood. This hinders, for example, the prediction of how and if PBAPs contribute to ice nucleation within clouds.

These uncertainties in atmospheric aging processes directly affect our understanding of PBAPs' role in cloud formation. Although PBAPs have been implicated in cloud formation and especially ice formation, their quantitative contribution within cloud processes remains highly uncertain. This is due to many reasons ranging from the overall lack of detailed *in situ* observations within clouds, high uncertainties in the various in-cloud processes involving ice (e.g., secondary ice formation, different freezing processes, etc.) but also due to the contribution of other aerosol sources facilitating formation of ice (e.g., dust). However, understanding how PBAPs interact with other atmospheric particles and how they influence cloud microphysics is crucial to assessing their role in regional and global climate systems.

The lack of detailed emission data for PBAPs from surface waters data with high spatial and temporal resolution is also an obstacle to developing a better representation of PBAPs within models. Current models often rely on generalized assumptions that may not adequately capture the complex dynamics of PBAPs from aquatic environments. In addition, integrating PBAPs into larger climate models is a challenging task. Most climate models do not fully account for the role of PBAPs in aerosol-cloud interactions, leading to a possible underestimation of their influence on radiative forcing and precipitation.

Already now, the fast development of new technologies is helping to constrain the role of surface water-driven PBAPs in the environment (Huffman *et al.*, 2020). For example, advanced optical or mass spectrometric methods that work in real-time or remote sensing techniques, such as fluorescence lidars, can help to increase our knowledge about the spatial distribution of PBAPs. In addition, emerging platforms such as drones or helikites can further help to increase spatial and vertical coverage for sampling PBAPs originating from surface waters. However, technological advances alone cannot address all these challenges. The study of PBAPs lies at the intersection between different disciplines. Addressing these challenges will require a better integration of research efforts between disciplines with multidisciplinary collaborations between biologists, atmospheric scientists, oceanographers, and researchers from both the experimental and the modeling world. Continuous bridging between fields will be essential for achieving a better and holistic understanding of the emission of PBAPs from surface waters and their impact on climate, the environment, and human health.

Literature cited

Aller J.Y., *et al.*, 2005. The sea surface microlayer as a source of viral and bacterial enrichment in marine aerosols. *J. Aerosol Sci.*, 36 (5-6), 801-812. https://doi.org/10.1016/j.jaerosci.2004.10.012

Alsante A.N., *et al.*, 2021. Ocean aerobiology. *Front. Microbiol.*, 12. https://doi.org/10.3389/fmicb.2021.764178

Amato P., *et al.*, 2023. The aeromicrobiome: The selective and dynamic outer-layer of the Earth's microbiome. *Front. Microbiol.*, 14, 1186847. https://doi.org/10.3389/fmicb.2023.1186847

Andreas E.L., *et al.*, 1995. The spray contribution to net evaporation from the sea: A review of recent progress. *Boundary-Layer Meteorology*, 72, 3-52. https://doi.org/10.1007/BF00712389

Blanchard D.C., Syzdek L.D., 1972. Concentration of bacteria in jet drops from bursting bubbles. *J. Geophys. Res.*, 77, 5087-5099. https://doi.org/10.1029/JC077i027p05087

Blanchard D.C., Syzdek L.D., 1982. Water-to-air transfer and enrichment of bacteria in drops from bursting bubbles. *Applied Environ. Microbiol.*, 43, 1001-1005. https://doi.org/10.1128/aem.43.5.1001-1005.1982

Burrows S., *et al.*, 2009. Bacteria in the global atmosphere–Part 2: Modeling of emissions and transport between different ecosystems. *Atmos. Chem. Phys.*, 9 (23), 9281-9297. https://doi.org/10.5194/acp-9-9281-2009

Burrows S.M., *et al.*, 2013. Ice nuclei in marine air: Biogenic particles or dust?. *Atmos. Chem. Phys.*, 13 (1), 245-267. https://doi.org/10.5194/acp-13-245-2013

Christiansen S., *et al.*, 2019. Sea spray aerosol formation: Laboratory results on the role of air entrainment, water temperature, and phytoplankton biomass. *Environ. Sci. Technol.*, 53 (22), 13107-13116. https://doi.org/10.1021/acs.est.9b04078

Cipriano R.J., 1979. Bubble and aerosol spectra produced by a laboratory simulation of a breaking wave. PhD Thesis, State University of New York at Albany.

Cipriano R.J., Blanchard D.C., 1981. Bubble and aerosol spectra produced by a laboratory 'breaking wave'. *J. Geophys. Res.: Oceans*, 86 (C9), 8085-8092. https://doi.org/10.1029/JC086iC09p08085

Cornwell G.C., *et al.*, 2023. Bioaerosols are the dominant source of warm-temperature immersionmode INPs and drive uncertainties in INP predictability. *Science Adv.*, 9 (37), eadg3715. https://doi.org/10.1126/sciadv.adg3715

Craig V.S., *et al.*, 1993. The effect of electrolytes on bubble coalescence in water. *J. Phys. Chem.*, 97 (39), 10192-10197. https://doi.org/10.1021/j100141a047

Cunliffe M., *et al.*, 2013. Sea surface microlayers: A unified physicochemical and biological perspective of the air-ocean interface. *Progr. Oceanogr.*, 109, 104-116. https://doi.org/10.1016/j.pocean.2012.08.004

Després V., *et al.*, 2012. Primary biological aerosol particles in the atmosphere: A review. *Tellus B*, 64 (1), 15598. https://doi.org/10.3402/tellusb.v64i0.15598

Döscher R., *et al.*, 2022. The EC-Earth3 Earth system model for the Coupled Model Intercomparison Project 6. *Geoscientific Model Development*, 15 (7), 2973-3020. https://doi.org/10.5194/gmd-15-2973-2022

Dubitsky L., *et al.*, 2023. Effects of salinity beyond coalescence on submicron aerosol distributions. *J. Geophys. Res.: Atmospheres*, 128 (10), e2022JD038222. https://doi.org/10.1029/2022JD038222

Fahlgren C., *et al.*, 2015. Seawater mesocosm experiments in the Arctic uncover differential transfer of marine bacteria to aerosols. *Environ. Microbiol. Reports*, 7 (3), 460-470. https://doi.org/10.1111/1758-2229.12273

Forestieri S., *et al.*, 2018. Temperature and composition dependence of sea spray aerosol production. *Geophys. Res. Lett.*, 45 (14), 7218-7225. https://doi.org/10.1029/2018GL078193

Freitas G., *et al.*, 2023. Regionally sourced bioaerosols drive high-temperature ice nucleating particles in the Arctic. *Nat. Commun.*, 14 (1), 5997. https://doi.org/10.1038/s41467-023-41696-7

Freitas G.P., *et al.*, 2022. Emission of primary bioaerosol particles from Baltic seawater. *Environ. Sci.: Atmos.*, 2 (5), 1170-1182. https://doi.org/10.1039/D2EA00047D

Gerardi M.H., Zimmerman M.C., 2004. *Wastewater pathogens*, John Wiley & Sons. https://doi.org/10.1002/0471710431

Harb C., *et al.*, 2021. Increasing freshwater salinity impacts aerosolized bacteria. *Environ. Sci. Technol.*, 55 (9), 5731-5741. https://doi.org/10.1021/acs.est.0c08558

Hartmann S., *et al.*, 2022. Structure and protein-protein interactions of ice nucleation proteins drive their activity. *Front. Microbiol.*, 13, 872306. https://doi.org/10.3389/fmicb.2022.872306

Hoose C., *et al.*, 2010. How important is biological ice nucleation in clouds on a global scale?. *Environ. Res. Lett.*, 5 (2), 024009. https://doi.org/10.1088/1748-9326/5/2/024009

Huffman J.A., *et al.*, 2020. Real-time sensing of bioaerosols: Review and current perspectives. *Aerosol Sci. Technol.*, 54 (5), 465-495. https://doi.org/10.1080/02786826.2019.1664724

Huffman J.A., *et al.*, 2013. High concentrations of biological aerosol particles and ice nuclei during and after rain. *Atmos. Chem. Phys.*, 13 (13), 6151. https://doi.org/10.5194/acp-13-6151-2013

Hultin K.A., *et al.*, 2011. Aerosol and bacterial emissions from Baltic Seawater. *Atmos. Res.*, 99 (1), 1-14. https://doi.org/10.1016/j.atmosres.2010.08.018

Janssen R.H.H., *et al.*, 2021. Drivers of the fungal spore bioaerosol budget: Observational analysis and global modeling. *Atmos. Chem. Phys.*, 21 (6), 4381-4401. https://doi.org/10.5194/acp-21-4381-2021

Knelman F., *et al.*, 1954. Mechanism of the bursting of bubbles. *Nature*, 173, 261. https://doi.org/10.1038/173261a0

Korzeniewska E., 2011. Emission of bacteria and fungi in the air from wastewater treatment plants–a review. *Front. Biosci. (Schol Ed)*, 3 (2), 393-407. https://doi.org/https://doi.org/10.2741/S159

Lang-Yona N., *et al.*, 2022. Terrestrial and marine influence on atmospheric bacterial diversity over the north Atlantic and Pacific Oceans. *Communications Earth & Environment*, 3 (1), 121. https://doi.org/10.1038/s43247-022-00441-6

Lewis E.R., 2006. The effect of surface tension (Kelvin effect) on the equilibrium radius of a hygroscopic aqueous aerosol particle. *J. Aerosol. Sci.*, 37 (11), 1605-1617. https://doi.org/10.1016/j.jaerosci.2006.04.001

Lewis E.R., Schwartz S.E., 2004. *Sea Salt Aerosol Production: Mechanisms, Methods, Measurements and Models*. The American Geophysical Union, 152, Geophysical Monograph Series. https://agupubs.onlinelibrary.wiley.com/doi/book/10.1029/GM152

Lighthart B., 1997. The ecology of bacteria in the alfresco atmosphere. *FEMS Microbiol. Ecol.*, 23 (4), 263-274. https://doi.org/10.1111/j.1574-6941.1997.tb00408.x

Lukas M., *et al.*, 2022. Toward understanding bacterial ice nucleation. *J. Phys. Chem. B*, 126 (9), 1861-1867. https://doi.org/10.1021/acs.jpcb.1c09342

Marks R., *et al.*, 2001. Bacteria and fungi in air over the Gulf of Gdańsk and Baltic sea. *J. Aerosol Sci.*, 32 (2), 237-250. https://doi.org/10.1016/S0021-8502(00)00064-1

Mårtensson E., *et al.*, 2003. Laboratory simulations and parameterization of the primary marine aerosol production. *J. Geophys. Res.*, 108(D9). https://doi.org/10.1029/2002JD002263

May N.W., *et al.*, 2016. Lake spray aerosol generation: A method for producing representative particles from freshwater wave breaking. *Atmospheric Measurement Techniques*, 9, 4311-4325. https://doi.org/10.5194/amt-9-4311-2016

May N.W., *et al.*, 2018. Aerosol emissions from great lakes harmful algal blooms. *Environ. Sci. Technol.*, 52 (2), 397-405. https://doi.org/10.1021/acs.est.7b03609

Mayol E., *et al.*, 2017. Long-range transport of airborne microbes over the global tropical and subtropical ocean. *Nat. Comm.*, 8 (1), 1-8. https://doi.org/10.1038/s41467-017-00110-9

Michaud J.M., *et al.*, 2018. Taxon-specific aerosolization of bacteria and viruses in an experimental ocean atmosphere mesocosm. *Nat. Comm.*, 9 (1), 2017. https://doi.org/10.1038/s41467-018-04409-z

Nielsen L.S., Bilde M., 2020. Exploring controlling factors for sea spray aerosol production: Temperature, inorganic ions and organic surfactants. *Tellus B: Chemical and Physical Meteorology*, 72 (1), 1-10. https://doi.org/10.1080/16000889.2020.1801305

Olson N.E., *et al.*, 2020. Harmful algal bloom toxins in aerosol generated from inland lake water. *Environ. Sci. Technol.*, 54 (8), 4769-4780. https://doi.org/10.1021/acs.est.9b07727

Paerl H.W., Huisman J., 2009. Climate change: A catalyst for global expansion of harmful cyanobacterial blooms. *Environ. Microbiol. reports*, 1 (1), 27-37. https://doi.org/10.1111/j.1758-2229.2008.00004.x

Pandey R., *et al.*, 2016. Ice-nucleating bacteria control the order and dynamics of interfacial water. *Science advances*, 2 (4), e1501630. https://doi.org/10.1126/sciadv.1501630

Park J.Y., *et al.*, 2014. Mixing state of submicrometer sea spray particles enriched by insoluble species in bubble-bursting experiments. *J. Atmos. Ocean. Technol.*, 31 (1), 93-104. https://doi.org/10.1175/JTECH-D-13-00086.1

Patterson J.P., *et al.*, 2016. Sea spray aerosol structure and composition using cryogenic transmission electron microscopy. *ACS Central Science*, 2 (1), 40-47. https://doi.org/10.1021/acscentsci.5b00344

Pendergraft M.A., *et al.*, 2023. Bacterial and chemical evidence of coastal water pollution from the tijuana river in sea spray aerosol. *Environ. Sci. Technol.*, 57 (10), 4071-4081. https://doi.org/10.1021/acs.est.2c02312

Perrott P., *et al.*, 2017. Preferential aerosolization of bacteria in bioaerosols generated in vitro. *J. Appl. Microbiol.*, 123 (3), 688-697. https://doi.org/10.1111/jam.13514

Pöhlker C., *et al.*, 2012. Autofluorescence of atmospheric bioaerosols – fluorescent biomolecules and potential interferences. *Atmos. Meas. Tech.*, 5 (1), 37-71. https://doi.org/10.5194/amt-5-37-2012

Price P.B., Sowers T., 2004. Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proc. Natl Acad. Sci. USA,* 101 (13), 4631-4636. https://doi.org/10.1073/pnas.0400522101

Pummer B., *et al.*, 2015. Ice nucleation by water-soluble macromolecules, *Atmos. Chem. Phys.*, 15 (8), 4077-4091. https://doi.org/10.5194/acp-15-4077-2015

Rahlff J., *et al.*, 2017. High wind speeds prevent formation of a distinct bacterioneuston community in the sea-surface microlayer. *FEMS Microbiol. Ecol.*, 93 (5), fix041. https://doi.org/10.1093/femsec/fix041

Rastelli E., *et al.*, 2017. Transfer of labile organic matter and microbes from th eocean surface to the marine aerosol: An experimental approach. *Sci. Rep.*, 7 (1), 1-10. https://doi.org/10.1038/s41598017-10563-z

Roeters S.J., *et al.*, 2021. Ice-nucleating proteins are activated by low temperatures to control the structure of interfacial water. *Nat. Comm.*, 12 (1), 1183. https://doi.org/10.1038/s41467-021-21349-3

Ruske S., *et al.*, 2017. Evaluation of machine learning algorithms for classification of primary biological aerosol using a new UV-LIF spectrometer. *Atmos. Meas. Tech.*, 10 (2), 695-708. https://doi.org/10.5194/amt-10-695-2017

Russell L.M., Singh E.G., 2006. Submicron salt particle production in bubble bursting. *Aerosol Sci. Technol.*, 40 (9), 664-671. https://doi.org/10.1080/02786820600793951

Salter M.E., *et al.*, 2014. On the seawater temperature dependence of the sea spray aerosol generated by a continuous plunging jet. *J. Geophys. Res.*, 119 (14), 9052-9072. https://doi.org/10.1002/2013JD021376

Salter M.E., *et al.*, 2015. An empirically derived inorganic sea spray source function incorporating sea surface temperature. *Atmos. Chem. Phys.*, 15 (19), 11047-11066. https://doi.org/10.5194/acp-15-11047-2015

Šantl-Temkiv T., *et al.*, 2022. Microbial ecology of the atmosphère. *FEMS Microbiology Reviews*, 46 (4), fuac009. https://doi.org/10.1093/femsre/fuac009

Sauer J.S., *et al.*, 2022. The sea spray chemistry and particle evolution study (SeaSCAPE): Overview and experimental methods. *Environ. Sci.: Processes Impacts*, 24 (2), 290-315. https://doi.org/10.1039/D1EM00260K

Schwier A.N., *et al.*, 2017. Primary marine aerosol physical flux and chemical composition during a nutrient enrichment experiment in mesocosms in the Mediterranean Sea. *Atmos. Chem. Phys.*, 17 (23), 14645-14660. https://doi.org/10.5194/acp-17-14645-2017

Seifried J.S., *et al.*, 2015. Spatial distribution of marine airborne bacterial communistes. *MicrobiologyOpen*, 4 (3), 475-490. https://doi.org/10.1002/mbo3.253

Seinfeld J., Pandis S., 2006. *Atmospheric chemistry and physics: From air pollution to climate change*, 2nd Ed., John Wiley and Sons, New Jersey.

Sesartic A., *et al.*, 2012. Bacteria in the ECHAM5-HAM global climate model. *Atmos. Chem. Phys.*, 12 (18), 8645-8661. https://doi.org/10.5194/acp-12-8645-2012

Sofieva S., *et al.*, 2022. Effects of temperature and salinity on bubble-bursting aerosol formation simulated with a bubble-generating chamber. *Atmospheric Measurement Techniques*, 15 (20), 6201-6219. https://doi.org/10.5194/amt-15-6201-2022

Spiel D.E., 1998. On the births of film drops from bubbles bursting on seawater surfaces. *J. Geophys. Res.*, 103, 24907-24918. https://doi.org/10.1029/98JC02233

Stokes M.D., *et al.*, 2013. A Marine Aerosol Reference Tank system as a breaking wave analogue for the production of foam and sea-spray aerosols. *Atmospheric Measurement Techniques*, 6 (4), 1085-1094. https://doi.org/10.5194/amt-6-10852013

Tian J., *et al.*, 2020. Real time detection and characterisation of bioaerosol emissions from wastewater treatment plants. *Sci. Tot. Environ*, 721, 137629. https://doi.org/10.1016/j.scitotenv.2020.137629

Tian J., *et al.*, 2022. Detection and characterization of bioaerosol emissions from wastewater treatment plants: Challenges and opportunities. *Front. Microbiol.*, 13, 958514. https://doi.org/10.3389/fmicb.2022.958514

Tyree C.A., *et al.*, 2007. Foam droplets generated from natural and artificial seawaters. *J. Geophys. Res.*, 112(D12). https://doi.org/10.1029/2006JD007729

Wang X., *et al.*, 2017. The role of jet and film dropsin controlling the mixing state of submicron sea spray aerosol particles. *PNAS*, 114 (27), 6978-6983. https://doi.org/10.1073/pnas.1702420114

WilsonT.W., *et al.*, 2015. A marine biogenic source of atmospheric ice-nucleating particles. *Nature*, 525 (7568), 234. https://doi.org/10.1038/nature14986

Wiśniewska K., *et al.*, 2022. Quantitative and qualitative´ variability of airborne cyanobacteria and microalgae and their toxins in the coastal zone of the Baltic Sea. *Sci. Tot. Environ*, 826, 154152. https://doi.org/10.1016/j.scitotenv.2022.154152

Woodcock A.H., 1953. Salt nuclei in marine air as a function of altitude and wind force. *J. Meteor.*, 10, 362-371. https://doi.org/10.1175/1520-0469(1953)010<0366:SNIMAA>2.0.CO;2

Woolf D.K., *et al.*, 1987. Discriminating between the film drops and jet drops produced by a simulated whitecap. *J. Geophys. Res.: Oceans*, 92(C5), 5142-5150. https://doi.org/10.1029/JC092iC05p05142

Zábori J., *et al.*, 2012. Artificial primary marine aerosol production: A laboratory study with varying water temperature, salinity and succinic acid concentration. *Atmos. Chem. Phys.*, 12, 10709-10724. https://doi.org/10.5194/acp-12-10709-2012

Zieger P., *et al.*, 2017. Revising the hygroscopicity of inorganic sea salt particles. *Nat. Comm.*, 8 (15883). https://doi.org/10.1038/ncomms15883

Zinke J., *et al.*, 2022. The effect of seawater salinity and seawater temperature on sea salt aerosol production. *J. Geophys. Res.: Atmospheres*, 127 (16), e2021JD036005. https://doi.org/10.1029/2021JD036005

Zinke J., *et al.*, 2024a. Quantification and characterization of microbial emissions over the northeastern Atlantic using mesocosm experiments. *ACS ES&T Air*, 1, 162-174. https://doi.org/10.1021/acsestair.3c00017

Zinke J., *et al.*, 2024b. Quantification and characterization of primary biological aerosol particles and microbes aerosolized from Baltic seawater. *Atmos. Chem. Phys.*, 24 (23), 13413-13428. https://doi.org/10.5194/acp-24-134132024

Chapter 8

Wildland fire smoke plumes as generators and transporters of living bioaerosols

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The origins of "pyroaerobiology"

The mechanisms by which terrestrial microbiomes become entrained and transported within or above the planetary boundary layer have traditionally focused on wind, dust storms, or point-source-driven emissions followed by horizontal and vertical turbulent mixing of air. Now, research has revealed a consequential new mechanism to add to the list of drivers of terrestrial-aerobiome microbial exchange: wildland fire (i.e. wildfires, prescribed burns, agricultural or biomass burning). In addition to the physical and chemical emissions in smoke, it is now understood that fires serve as ubiquitous sources of aerosolized viable microbes, yielding near-field concentrations and diversity that significantly exceed background levels (Mims and Mims, 2004; Kobziar *et al.,* 2018, 2022, 2024b; Moore *et al.,* 2020). As wildfire frequency and severity in many regions continue to increase with global climate change (Jones *et al.,* 2022), the microbial content of smoke is a pressing and timely consideration.

Globally, biomass burning emits an annual average of 85 Tg of particulate matter (PM) into the atmosphere (Andreae, 2019), which is composed of highly oxidized organic materials, incomplete combustion products, and mineral content (Bormann *et al.,* 2008) as fires can aerosolize both soil and plant organic and inorganic materials (Pisaric, 2002; Kobziar *et al.,* 2022). Although considerable research has focused on the aerosolization and atmospheric movement of microbes in clouds (Brown and Hovmøller, 2002; Griffin, 2007) and on pollution-borne PM (Boreson *et al.,* 2004; Frohlich-Nowoisky *et al.,* 2009; Barberán *et al.,* 2015), only recently have scientists become aware of the capacity for smoke from biomass fires to act as a vector for viable bacteria and fungi dispersal (Kobziar *et al.,* 2024b). Smoke from large or long-burning wildfires can be transported around the world (Dirksen *et al.,* 2009), suggesting that its microbial cargo may be included in the journey attached to or free from PM. This topic has gained significant attention as much of the world is encountering increased severity and longevity of smoke events from wildfire activity (Hung *et al.,* 2020; Kobziar and Thompson, 2020; Tencé *et al.,* 2022).

Aerosolization and transport of microbes through smoke from wildland fires was first reported as an inference drawn from backyard observations conducted by a teenager working with her father (Mims and Mims, 2004). As an atmospheric scientist, Dr. Forrest Mims helped his daughter design a low-cost, high-impact experiment for a 2004 high school science fair contest, and the results and implications earned her the top prize for reasons that became clearer over a decade later[5]. Mims observed that fungal spore concentrations were higher when charcoal-like PM was present on her microscope slides, and using a back trajectory analysis, deduced that traveling smoke from biomass burning over 1000 km away was responsible. Some additional campfire-type burns in the Mims' backyard confirmed that fungal colony abundance was higher with than without smoke, which crystallized the hypothesis that wildland

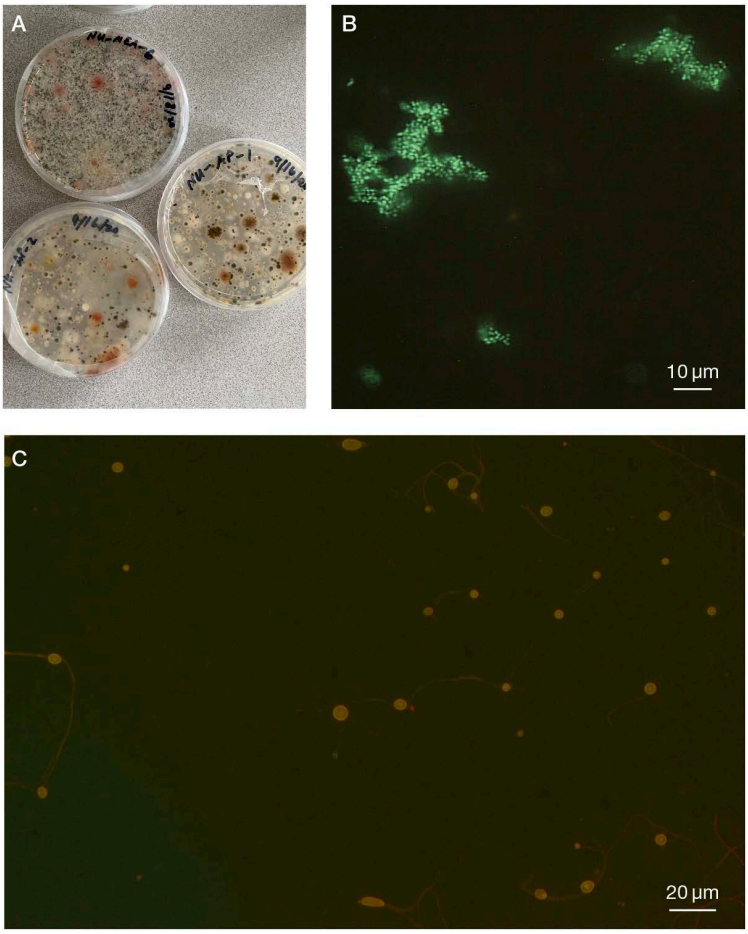

Figure 8.1. Macroscopic and microscopic view of microorganisms captured from fire plumes.

A. Fungal and bacterial cultures developed on malt extract agar four days post-sampling in smoke from biomass burning. **B.** Epifluorescence microscopy images of bacterial cells stained with Syto-9/Propidium Iodide. **C.** Fungal hyphae and spores extracted from filter-based smoke samples and stained with Calcoflour White (Kobziar, Bonfantine and Lampman, *unpublished data*).

5. https://earthobservatory.nasa.gov/features/SmokeSecret

fire was at least a local vector for fungal spore emission. Surprisingly, no subsequent studies sought to test the hypothesis, neither through experimental nor observational means, for over a decade after the Mims and Mims study.

In 2015, Heather Larson, then at the University of Florida, was searching for a topic for a final project for her master's degree and pursued her fire ecology professor's curiosity about smoke: could it contain more than abiotic byproducts of incomplete combustion (i.e. ash, soot, and gases)? They exposed petri plates (like those shown in Figure 8.1) to smoke from burning understory fuels (grasses and shrubs) at various distances upwind and downwind of active combustion, both flaming and smoldering, across a few different ecosystems and fire regimes during local prescribed burns. The results were unequivocal: smoke produced higher concentrations of and more diverse bacterial and fungal colonies closer to the source of fire, and hardly any upwind (Kobziar *et al.,* 2018). The work generated numerous related questions and hypotheses about the mechanisms, patterns, and implications of smoke transport of living microbes, and the study of "pyroaerobiology" was born.

⏩ Doesn't fire kill microbes?

Microbiology's earliest tools included a wire loop for transferring colonies from microbiological media and a flame for sterilization, so the role of fire as a vector for living bacteria and fungi is somewhat counterintuitive. In fact, even in most modern texts dealing with the ecological role of fire, a rule-of-thumb for thermal mortality has for decades been that exposure of living things to 60°C for 1 minute would lead to mortality. This threshold is widely used in modeling systems to determine fire effects and fuels consumption on plants and other organisms (BEHAVE, FOFEM, CONSUME[6]; Prichard *et al.,* 2014). Yet, the translatability of its derivation (original studies were on disconnected tree needles) and its legitimacy are suspect, especially in light of the diversity of microbes that survive high temperature dosages and even thrive in the wildland fire environment (Glassman *et al.,* 2016; Kobziar *et al.,* 2018; Pingree and Kobziar, 2019; Kobziar *et al.,* 2019; Moore *et al.,* 2020; Kobziar *et al.,* 2022; Fox *et al.,* 2022). Certain fungi, such as *Anthracobia melaloma*, some *Aspergillus* spp., and some *Penicillium* spp., rely on fires for spore germination whereas others can take advantage of the convective forces produced by heat and smoke, enabling them to spread spores over vast distances, potentially colonizing new areas (Fox *et al.,* 2022). The contradiction between observations of pyrophilic fungi (e.g., Glassman *et al.,* 2016) or at the very least pyro-agnostic microbes and a temperature mortality threshold that is lower than what even soil microbes may be subjected to (Busse *et al.,* 2013; Kreye *et al.,* 2020) inspired a review of microbial tolerance to thermal stress. Researchers performed a comprehensive meta-analysis of published data that compared soil/rhizosphere microbial tolerance to various heat dosages against controls to find that fungal and bacterial tolerances ranged significantly depending on the organisms and study design (Pingree and Kobziar, 2019). Importantly, neither fungi- nor bacteria-derived evidence pointed to a consistent mortality threshold, with mortality occurring at ranges from 60°C to 400°C for fungi and 80°C to 400°C for bacteria over 2–30 min durations (Pingree and Kobziar, 2019).

6. BEHAVE: https://research.fs.usda.gov/firelab/products/dataandtools/behaveplus; FOFEM: https://research.fs.usda.gov/firelab/products/dataandtools/fofem/spatialfofem-fire-effects-model; CONSUME: https://research.fs.usda.gov/pnw/projects/consumesoftware.

With these ranges of thermal tolerance and the high degree of temperature variability within burned areas (especially at the scale of a microbe), it should not be a surprise that studies have found that the viability of the microbes found in smoke is not that different from that of bioaerosols under ambient conditions. Viability of smoke-borne organisms has been inferred through cell-staining techniques that distinguish living cells (Figure 8.1B and 8.1C; Moore *et al.,* 2020; Kobziar *et al.,* 2022; Ellington *et al.,* 2024) and through the culturing of fungi and bacteria from smoke samples (Mims and Mims, 2004; Kobziar *et al.,* 2018; Mirskaya and Agranovski, 2020; Moore *et al.,* 2020). Furthermore, laboratory experiments have confirmed successful translocation of functioning microbes from vegetation, through smoke, into soils (Ellington *et al.,* 2024). However, the long-term and long-distance survival of microbes in smoke requires additional surveys. It also remains to be determined how abiotic factors such as ultra-violet radiation and high levels of ozone might influence microbial activity during transport, during both ambient and smoke conditions.

⏩ Methods from the ground to the sky

Original aerobiological sampling (Hirst, 1952) and early capture of wildland smoke for detection of microbes (Mims and Mims, 2004; Kobziar *et al.,* 2018) were completed using passive sampling from ground-based platforms directly onto growth media. Opportunistic sampling on stationary platforms is a challenge due to limited or unpredictable interaction with smoke plumes, and inherently hazardous conditions near wildland fires. Although satellite observations can track smoke in the atmosphere, smoke at ground level is difficult to trace with specificity to distant sources when ground-based observations are lacking. Adequate capture of wildland fire smoke requires nimble and mobile sampling platforms that can respond quickly to the changes in wind direction or fire behavior that dictate smoke patterns. Use of uncrewed aircraft systems (UAS) to capture bioaerosols has been demonstrated in the ambient environment, for example, above crop fields to collect plant pathogen propagules (Aylor *et al.,* 2011; Schmale *et al.,* 2012). Recent innovation in the use of mobile sampling platforms has accelerated, and UAS are now being deployed within wildland fire plumes to sample at various altitudes and distances downwind of a fire, all while keeping the operators out of harm's way (Aurell *et al.,* 2015, 2021; Villa *et al.,* 2016; Nelson *et al.,* 2019). By initiating UAS as a platform for customized bioaerosol sampling payload during turbulent flight, Kobziar *et al.* (2019) documented a higher concentration of viable organisms within the smoke plume relative to ambient air. Following this demonstration, UAS equipped with composite sampling packages, including various combinations of microbial samplers, micrometeorology sensors, carbon sensors, and elemental carbon impactors are now being used to circulate through wildland smoke plumes for capture of bacterial and fungal cells/spores (Kobziar *et al.,* 2022, 2024b; Bonfantine *et al.,* 2024). The microbial sampling strategy uses compensating vacuum pumps attached to filter-based samplers (with screens to exclude abiotic particulates >100 μm) to characterize wildland fire plume microbiomes. Airborne capture of smoke's bioaerosols onto Teflon or polycarbonate filters and subsequent elution and purification has demonstrated the production of sufficient quantities of usable DNA for amplicon sequencing and taxonomic identification (Kobziar *et al.,* 2022, Bonfantine *et al.,* 2024).

Incorporation of micrometeorological data during microbial sampling flights enables researchers to explore relationships between variables such as temperature and relative humidity, known to influence aerobiome composition (e.g., Almeida *et al.,* 2018), and the microbial assemblages identified from smoke and background samples. How much these factors influence the smoke aerobiome remains unknown, but limited data suggest that higher temperatures and relative humidity in smoke correspond to higher concentrations of bacterial cells (Kobziar *et al.,* 2022). In addition to micrometeorological data, gas and carbon measurements are essential for understanding and modeling microbial emissions from wildland fires. By analyzing major carbon components in smoke –such as carbon monoxide (CO), carbon dioxide (CO_2), and total carbon (TC)– researchers can determine the combustion phase (e.g., smoldering vs. flaming) of the burning area from which microbes were released using modified combustion efficiency (Yokelson *et al.,* 1996). These carbon concentrations also provide insight into the number of microbes emitted per unit mass of biomass fuel burned, values known as emission factors (EFs), further explained below (Kobziar *et al.,* 2024b). To investigate how the EFs, concentration, and viability of microbes in wildland fire smoke change during their transport, multiple UAS can be utilized at various distances downwind in the smoke plume (Figure 8.2). UAS equipped with

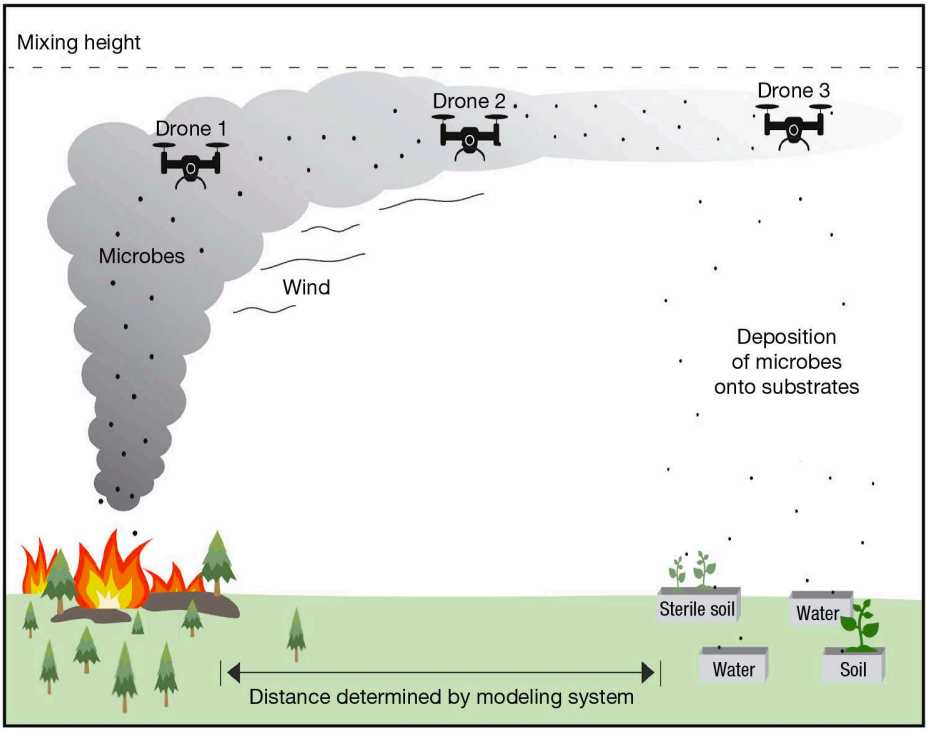

Figure 8.2. Deploying multiple aerial sampling systems simultaneously at different altitudes and distances from a fire enables quantification of distance decay changes in microbial composition, emission factors, concentrations, and viability. Coupled with ground-based sampling, plume transport and deposition-driven dispersal can be characterized in relation to fire behavior and atmospheric factors. Higher-intensity wildfires frequently move smoke above the planetary boundary layer resulting in longer-distance transport.

thermal infrared cameras can capture fire behavior metrics –such as rate of spread and intensity– that help explain how different fire conditions influence the emission rates and patterns of smoke microbial content.

The DNA captured from smoke and concentrated on filters can be extracted and characterized using next-generation sequencing technologies. The taxonomic identity of the smoke-borne organisms is determined through amplicon sequencing using phylogenetically informative markers for prokaryotes and eukaryotes, such as 16S and ITS ribosomal loci, respectively. The amplicon library preparations and data analyses can follow established methods with special emphasis on collecting abundant negative controls due to the low biomass nature of air samples (Reichman *et al.,* 2021; Miaow *et al.,* 2021). Amplicon sequencing of smoke samples shows that not only are there up to ten times more organisms in smoke than in ambient air, but smoke contains a higher diversity of assemblages (Kobziar *et al.,* 2022). The adaptation of 16S amplicon sequencing for source-tracking of prokaryotes mobilized by wildland fire smoke was demonstrated by Bonfantine *et al.* (2024) and is discussed further below. If only certain taxa are of interest, such as specific pathogens with known environmental reservoirs susceptible to aerosolization during wildland fires (see Table 8.1), quantitative PCR can be used. One such example is the CocciENV assay that was designed for detection of *Coccidioides immitis* and *Coccidioides posadasii*, the causative agents of Valley fever (Bowers *et al.,* 2019).

From identifying the players to understanding the rules, metagenomic and metatranscriptomic methods present yet unexplored opportunities to investigate the structure and function of the pyroaerobiome. The potential of these approaches is constrained by the methodological and environmental challenges posed by sampling bioaerosols, including the low density, inefficient recovery, and inherent spatial and temporal variability of airborne assemblages (Behzad *et al.,* 2015). Overcoming these hurdles is important because improved understanding of the metabolic strategies and functional guilds within the smoke environment will help to clarify the role of smoke as a microbial reservoir and dispersal vector. Understanding how microbes survive and interact in smoke will also help to inform a fundamental question for pyroaerobiology and aerobiology more generally – is the atmosphere an ecosystem (Lappan *et al.,* 2024)?

⏩ What goes up in smoke?

Sampling of wildfire plumes at various altitudes indicates that smoke is both a convective and a dispersive force affecting a range of microbial taxa, from bacteria to microeukaryotes. The conceptual framework for the composition of smoke microbes is depicted in Figure 8.3, which shows that the relationships between combusted sources, smoke, and the surrounding ambient air microbiome are likely a function of fire behavior, weather conditions, and factors affecting deposition. What determines the thresholds for smoke microbial signal detection as smoke travels away from the burn zone has yet to be elucidated and likely differs for different fires and atmospheric conditions (Figure 8.3). The distance of detectable microbial transport through smoke depends on many factors including fire intensity, plume height, atmospheric factors, and weather nearby and downwind. In addition, the relationship between source fuels burned and fire behavior likely determines the physical characteristics of microbial clusters and PM, aggregation and disaggregation processes as smoke ages, and

deposition patterns (Inci *et al.,* 2017; Kobziar *et al.,* 2024b). While smoke often reaches temperatures exceeding the natural limits of most thermophiles, it also entrains and transports ambient air, water vapor, organic matter, and other particulates that may play a role in protecting viable microbes (Chapter 5; Kobziar *et al.,* 2018, 2022). In one high-intensity forested fire regime, taxonomic analysis of smoke-borne microbes indicated that 70% of sampled microbes in smoke can be traced to terrestrial sources, in contrast with 42% in ambient air (Bonfantine *et al.,* 2024). The highest percentage of these smoke microbes was linked to soil sources, followed by vegetative fuels (Bonfantine *et al.,* 2024). Wildland fire also multiplies aerosolized microbial cellular concentrations, with one study estimating that for each hectare burned, wildfire in the western USA contributes 3.71×10^{14} bacterial cells and alters the microbial taxonomic richness of the local atmosphere (Kobziar *et al.,* 2024b). This estimate gives pertinent context for experiments to measure emissions as described in Chapter 3. Furthermore, when compared to emissions of spores of rusts from diseased fields of wheat or perennial rye grass during harvest combining (ca. 10^{13}/ha; Morris *et al.*, 2013), this estimate reveals the exceptional strength of wildfires as a source of bioaerosols.

The smoke microbiome encompasses various eukaryotes, including a diversity of fungi, plus a wide range of prokaryotes, including the archaeal phylum, Thaumarchaeota, which contains a number of hyperthermophiles (Kobziar *et al.,* 2022). Some smoke-borne microbiota may possess traits making them resilient to extreme heat,

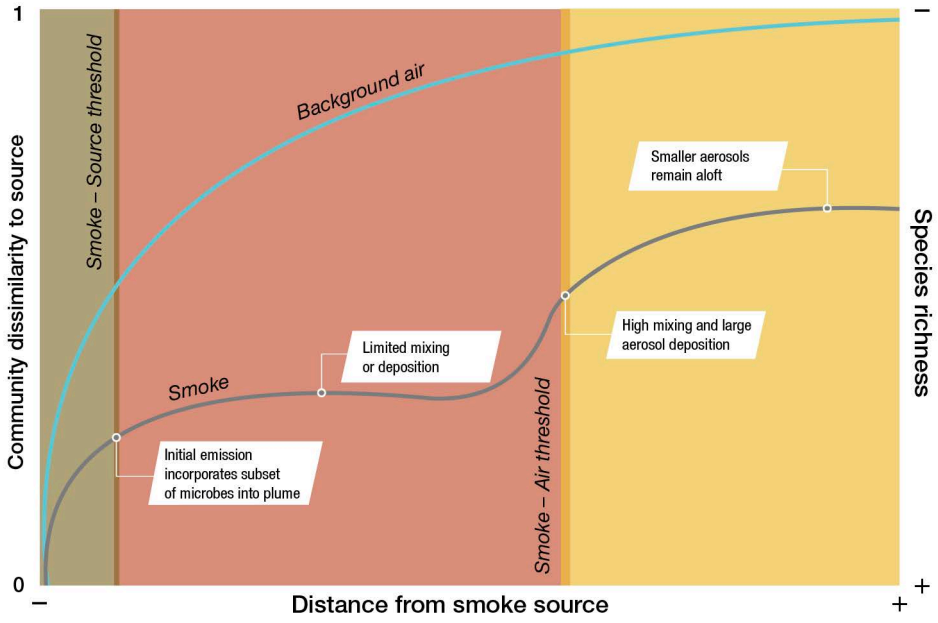

Figure 8.3. Conceptual diagram showing how species richness (right y-axis) and composition of smoke bioaerosols (left y-axis) are functions of the distance from the fuel source, with terrestrial-sourced bioaerosols more abundant closer to the fire, and background bioaerosols playing a larger role in community composition beyond a "smoke-air threshold". The scale of the x-axis depends on fire regimes, locations, and atmospheric conditions as well as real-time fire behavior driving combustion efficiency and smoke plume transport (Kobziar, Bonfantine and Lampman, *unpublished data*).

smoke, ultraviolet radiation, and other characteristics of wildland fires, while others may exploit pockets of ambient air, water vapor, or organic matter carried by smoke (so-called "smoke refugia") (Kobziar *et al.*, 2018, 2024a; Kobziar and Thompson, 2020). Additional analyses are required to determine whether smoke-borne microbes are interacting and functioning as a bioaerosol community or simply in the same place at the same time.

The composition of the smoke microbiome varies across space and time, with regional and seasonal patterns. The enrichment of Gammaproteobacteria in smoke samples from Kansas, USA (Figure 8.4A) reflects the native tallgrass prairie community (vegetation and soils) at the burn location. In contrast, smoke samples from other regions are enriched with Actinobacteria which could reflect differences in the combusted vegetation or a higher level of soil mobilization during more intense burning and convective conditions. It is postulated that preferential aerosolization may be occurring, since Actinobacteria possess morphological traits that can facilitate aerosolization

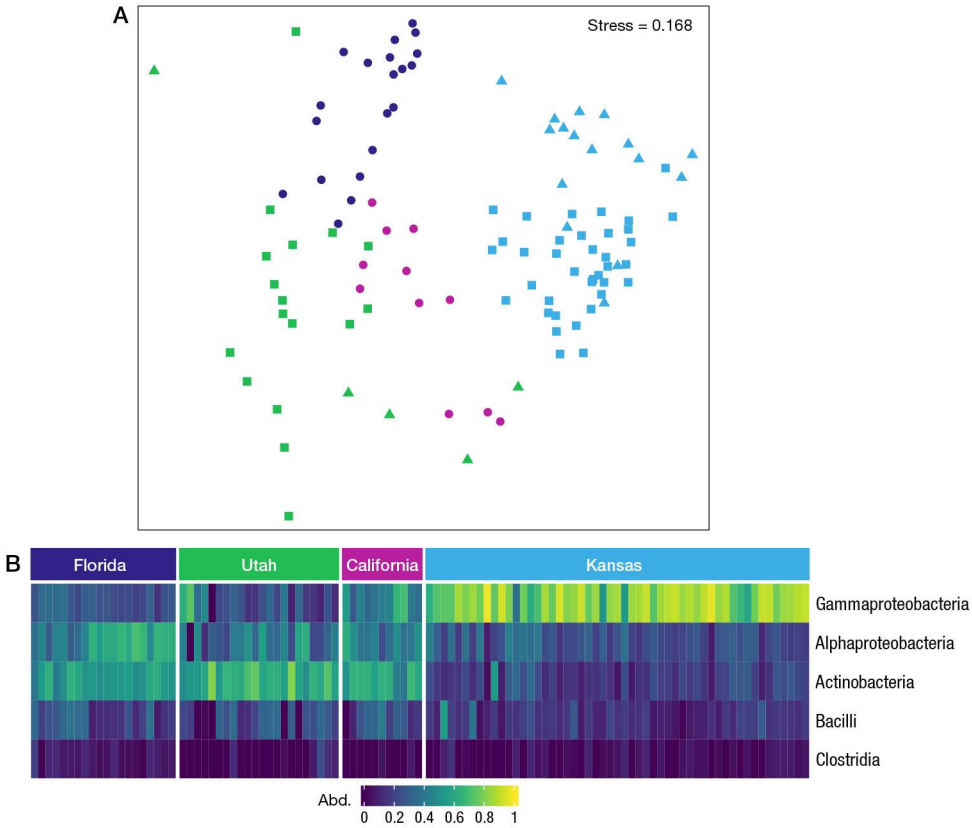

Figure 8.4. A. Non-metric multidimensional scaling plot of Bray-Curtis distances among Hellinger-transformed bacterial assemblages in smoke samples collected from fires across four states. Different symbols of the same color (e.g., green for Utah) reflect seasonal differences in two states where fires were sampled in both spring and fall. **B.** Heatmap showing the Hellinger-transformed abundance of the five most abundant bacterial classes across four states. These results suggest that both location and season are strong drivers in distinguishing smoke aerobiomes across vegetation types and locations. (Kobziar, Bonfantine and Lampman, *unpublished data*).

(Kobziar *et al.,* 2022). However, at the moment of emission, the limited data that exist suggest that fire is an equal-opportunity force, rather than a selective player targeting fire-tolerant species (Kobziar *et al.,* 2022).

The concentration of smoke-borne microbes diminishes at increasing distance from the fire, as smoke mixes with the surrounding air and these airborne microbes are deposited on land (Kobziar *et al.,* 2018).

⏩ Hot on the trail: Tracking the journeys of smoke plumes and microbes

In addition to the molecular characterization of the smoke microbiome, additional understanding of pyroaerobiology can be inferred from other areas of smoke science. Tracing the path of smoke from its point of origin is facilitated through a suite of established and emerging tools that combine ground-based measurements, models, and satellite observations. Atmospheric transport models, such as HYSPLIT (Hybrid Single-Particle Lagrangian Integrated Trajectory), which correlate an air parcel to a likely region of origin, provide a mechanism to link observed phenomena in distant ecosystems back to a fire location. Use of such transport models as part of the toolbox for assessing dispersal of bioaerosols and small insects is described in detail in Chapter 11. Studies detailing smoke plume dynamics and resulting atmospheric turbulence therefore also describe the conditions affecting dispersal of smoke-borne microbes (Kobziar *et al.,* 2024b).

The chemical constituents of smoke provide another means of tracking the path of a smoke plume and the microbes contained within. Smoke plumes typically contain elevated levels of inorganic nutrients such as iron (Perron *et al.,* 2022). Unique ratios of inorganic ions can reflect the source of the combusted vegetation (Simoneit, 2002) and can serve as a molecular fingerprint to chronicle smoke's journey. Combined with measurements of organic biomarkers, nutrient and particulate levels can be associated with ecological impacts. In addition to PM (McCluskey *et al.,* 2014) and organic carbon, common tracers of biomass combustion include water-soluble potassium and levoglucosan, which is formed by the degradation of cellulose during burning (Simoneit, 2002; Zhang *et al.,* 2008). Concentrations of bacteria within bioaerosols have been positively correlated with PM_{10} and show three-fold higher cell concentrations per μg PM_{10} in smoke than in ambient air (Moore *et al.,* 2020). Bacterial cell concentrations were also positively correlated with levels of organic carbon and potassium derived from biomass burning (Rajput *et al.,* 2017). Elevated levels of water-soluble potassium and levoglucosan during biomass burning events have also been positively correlated with levels of the fungal biomarkers, arabitol and mannitol (Yang *et al.,* 2012; Tyagi *et al.,* 2016), as well as elevated atmospheric concentrations of hydroxy fatty acids (Tyagi *et al.,* 2016).

Fire emission and atmospheric transport models provide valuable insights into where smoke and its associated aerosols are transported. However, to achieve a more comprehensive understanding of the microbial components in smoke and their transport, it is essential to know the number of microbes emitted per mass of biomass fuel burned, or microbial EFs. Emission factors vary widely based on many different variables and can be distinguished by fire phase (e.g., smoldering vs. flaming), fuel type,

and measurement approach (Prichard *et al.,* 2020). They are widely used in smoke models to predict the emission and transport of aerosols (Reinhardt *et al.,* 1997; Prichard *et al.,* 2014; Stein *et al.,* 2015). Microbial EFs have the potential to enable researchers to examine critical questions relating to pathogen transport (Aylor *et al.,* 2011; Kobziar and Thompson, 2020; Hauser *et al.,* 2021), the influence of microbial dispersal on biodiversity (Pearce *et al.,* 2016), impacts on ecosystem function (Smith *et al.,* 2011), and the role of microbes in atmospheric processes, including cloud or ice nucleation (Bauer *et al.,* 2003; Moore *et al.,* 2020; Kobziar *et al.,* 2022). Microbial emission factors are the link required to model and scale up measures from single fires to global estimates for fire-driven emission of microbes.

The current approach for determining microbial emission factors relies on the carbon mass balance method. In this approach, the total mass concentration of carbon (both in gaseous and particulate forms) in smoke is estimated to represent roughly half of the biomass consumed during combustion (Williams *et al.,* 2017). Microbial concentrations can then be normalized against these major carbon constituents, allowing for an estimate of microbial emissions relative to the biomass fuel consumed. This was done for a high-intensity subalpine wildland fire, where Kobziar *et al.* (2024b) calculated an emission factor of 7.68×10^{11} bacteria emitted for each Mg of biomass consumed. This scales to an annual emission of approximately 1.35×10^{17} cells, or 8.1 kg of bacterial biomass, from the ~2,631 hectares of similar forests in Fishlake National Forest that burn on average each year. Using a particle transport model with a prediction area of 17.25 × 17.25 km centered on the fire, they further estimated that less than 0.05% of the aerosolized bacteria would be deposited within the model's prediction area, meaning the bacteria were being transported longer distances. As microbial EFs are developed for different environments –accounting for specific fuels, fire behaviors, and combustion phases– and incorporated into various emission and atmospheric transport models, researchers will be able to address key questions about microbial emissions and transport in wildland fires.

⏩ What are the implications?

Microbial emissions in smoke have implications for biodiversity, infectious disease, atmospheric dynamics, and the myriad ways that microbes function in human and natural systems. Depending on the intensity of the fire, the fuels and soils being burned and exposed to convective winds, and the proximity of the source to regions experiencing deposition, smoke may act as a vector of dispersal, and/or a source of nutrients such as nitrogen, phosphorus, and sulfur (Barkley *et al.,* 2019; Koplitz *et al.,* 2021; Zhu *et al.,* 2024). Microbes dispersed by smoke from wildland fires can affect atmospheric conditions while aloft and can affect environments where they are deposited, potentially influencing soil health, water quality, and terrestrial communities. The ecological impacts of pyroaerosolization and deposition are likely related to the frequency of fire (and smoke) in the receiving ecosystem. In frequent-fire systems, fire has presumably been transporting microbes for as long as the systems have existed, and smoke's role may be to provide a temporary refuge for microbes with less pronounced impact upon deposition in similar ecosystems. For example, fire is a yearly occurrence across millions of hectares of global grasslands, so the fire-smoke-terrestrial microbe relationships would be part of an established, cyclical and even integral relationship with

disturbance (Kobziar *et al.,* 2024a). On the other hand, in regions with infrequent fire regimes or where receiving substrate conditions are conducive to colonization (e.g., low competition; Ellington *et al.,* 2024), the introduction of new microbes may represent a more significant disruption, pushing the host microbial community toward a new equilibrium (Kobziar *et al.,* 2024a). This open question is especially intriguing when considering infrequent or changing fire regimes. For example, deep organic fuels, such as thawed permafrost soils, are becoming available for combustion due to climate change, so fire has the potential to aerosolize and transport microbiota that have been sequestered for thousands of years (Alempic *et al.,* 2023).

Atmospheric consequences

Microbial bioaerosols act as ice nuclei, facilitating the formation of ice crystals and the development of mixed-phase clouds (Morris *et al.,* 2014). These ice nucleating particles (INPs) aid in cloud condensation or glaciation, precipitation and water transport, and may play a role in microbial dispersal (Christner *et al.,* 2008; Spracklen and Heald, 2014; Kobziar *et al.,* 2022). An experimental study during prescribed burns in Florida, USA, noted that the biological INPs in aerosols were higher within smoke relative to ambient controls, and further used cultivation to demonstrate their viability and infer soil as their terrestrial source (Moore *et al.,* 2020). In a contrasting ecosystem and higher intensity crown fire, researchers found corroborating results: INPs were higher in smoke than in ambient air, and their sources were predominantly biological (Kobziar *et al.,* 2022). Other aerosol studies focused on wildfire smoke chemistry have yielded similar results, but did not investigate microbial content specifically (e.g., Barry *et al.,* 2021). Depending on the concentration of these INPs, a region may experience rapidly cooler conditions, diminished radiative forcing, and a sudden increase in chance of precipitation, with potentially global ramifications (DeMott *et al.,* 2010; Barry *et al.,* 2021). Quantifying and identifying fire-driven microbial INPs further couples atmospheric, terrestrial, and aquatic ecosystems in locations of high wildland fire incidence.

Ecological consequences

The deposition of smoke's bioaerosols back to terrestrial ecosystems can occur throughout the smoke's journey, both adjacent to and within burned regions. Smoke bioaerosols can change taxonomic and functional community composition through either wet (e.g., precipitation) or dry deposition (e.g., sedimentation). Wet deposition can be facilitated by condensed water droplets, most often by precipitation but in some cases through the condensation of mist or fog on terrestrial surfaces (Morris *et al.,* 2008; Woo and Yamamoto, 2020). The path of smoke-borne microbes back to terrestrial or even aquatic systems has yet to be extensively traced, but one field-based study provides insights. Bonfantine *et al.* (2024) used molecular source tracking to estimate that smoke contributed 30% and 25% of the soil and local tree phyllosphere bacterial microbiomes, respectively, downwind of a forest fire. In fire-prone regions, it is unlikely that the microbiomes of sources and sinks are independent, given that fire has influenced microbial exchange between the terrestrial and atmospheric microbiomes for thousands of years.

The microbial transfer from smoke-derived bioaerosols to terrestrial ecosystems has also been documented for soils under laboratory conditions (Ellington *et al.,* 2024).

Native and gamma-irradiated soils were inundated with various levels of smoke in the laboratory to simulate undisturbed and highly disturbed soils (Ellington *et al.,* 2024). Ten days following the smoke exposure, source tracking indicated that 30% of the microbial community that developed in the irradiated soils could be traced to smoke, with less than 3% associated with ambient, background air and the remainder classified as having an unknown source. The smoke-driven microbial deposition triggered increased soil respiration rates compared to pre-treatment conditions. This response was especially pronounced in the disturbed soils, where earlier peak respiration rates were also associated with smoke treatments containing higher concentrations of viable cells (Ellington *et al.,* 2024). The transmission of microbes carried in wildland fire smoke may therefore represent a previously overlooked component of disturbance recovery in burned soils. Enrichment of Frankiales and nitrogen-fixing archaea in smoke bioaerosols (Kobziar *et al.,* 2022; Bonfantine *et al.,* 2024) suggests that smoke can deposit beneficial microbes downwind. Smoke may also transfer nutrient-conducting mycorrhizal fungi into burned or otherwise disturbed soils (Figure 8.1C).

Deposition of smoke-borne microbiota into downwind aquatic and marine ecosystems has been reported by researchers using a real-time bioaerosol autofluorescence sensor during smoke episodes from massive peat fires in Indonesia (Yue *et al.,* 2025). Such transport may also be inferred from studies that have documented nutrient additions from smoke. Nutrients like phosphorous can be thousands of times more elevated in smoke (Olson *et al.,* 2023), and there are widespread fire-related increases in aquatic total phosphorous concentrations, particularly in oligotrophic systems, which may be explained by deposition from atmospheric sources including biomass burning (Stoddard *et al.,* 2016; Yue *et al.,* 2025). Nitrogen and phosphorous enrichment have been measured in multiple freshwater ecosystems that were exposed to smoke but not directly impacted by fire (Spencer and Hauer, 1991; Earl and Blinn, 2003; Evans *et al.,* 2021; Olson *et al.,* 2023). Likewise, iron-rich smoke plumes have been implicated in the initiation of algal blooms (Olson *et al.*, 2023) in the Southern Ocean (Tang *et al.,* 2021), and wildfire-derived nitrogen was linked to an Arctic phytoplankton bloom (Ardyna *et al.,* 2022). These transmissions of inorganic nutrients from smoke to freshwater and marine ecosystems have almost certainly occurred in tandem with a transfer of biological material but it remains unknown what proportion of deposited organisms survive and/or shift the receiving microbiomes. Likewise, Wang *et al.* (2022) found that the precipitation-induced deposition of biogenic carbon and macronutrients from smoke may have caused massive phytoplankton blooms in marine ecosystems in the Atlantic Ocean in 2019-2020, illustrating the close integration between smoke aerosols and the hydrologic cycle.

Like in soil ecology, microbial deliveries from smoke would likely have the greatest impact on aquatic ecosystems that were not historically exposed to a particular microbial assemblage in smoke, or those that are more susceptible to colonization impacts. An alternative perspective might posit that some aquatic ecosystems embedded in frequent fire landscapes, having been impacted by surrounding fire for millennia, are adapted to the regular chemical, physical, and likely biological exchanges with smoke. Deposition of INPs, viable microbes, biogenically active carbon, and key macronutrients into oceans, freshwater lakes, or streams, for example, may shape the biodiversity or function of an ecosystem (Yue *et al.,* 2025).

In cases where smoke travels long distances, the transported microbes may represent new additions to the ecosystem with an ability to thrive dependent on any competitive advantages they might have over native microbes (Pretorius *et al.,* 2023). The impact of these introductions can be significant, especially if the new microbes possess traits that allow them to exploit local resources effectively. Shifts in microbial community structure may have commensurate shifts in function, leading to changes in nutrient cycling, plant interactions, decomposition rates, and enzymatic activity (Harris, 2009; Fierer *et al.,* 2010; Zhong *et al.,* 2018; Zhou *et al.,* 2022).

Polar ecosystems hold perhaps the most potential for change related to the increasing frequency and duration of smoke events. Biological deposition has been associated with dust events in Antarctica (Michaud *et al.,* 2014) but not yet specifically associated with smoke. Airborne connectivity was previously described as largely localized in Antarctica (Archer *et al.,* 2019) but the detection of smoke from the 2019/2020 bushfires in Australia 20 days after the fires (Tencé *et al.,* 2022) highlights smoke as a potential source of biological intercontinental connectivity between distant biomes. Smoke deposition affects polar albedo and ice melting through the physical deposition of smoke-borne particulate matter (Aubry-Wake *et al.,* 2022; Tencé *et al.,* 2022) but bioaerosol deposition may also contribute by altering the microbial structure and function in cryoconite depressions and soils. The unique biomes of polar regions are considered particularly vulnerable to an influx of foreign and invasive taxa due to changes in temperature and atmospheric circulation patterns as a result of climate change (Archer *et al.,* 2019), which is also driving increased global fire activity.

Pathogen dispersal

In addition to the manifold impacts of microbial aerosolization as a driver of biogeography, atmospheric transport of microbes can affect human, animal, and plant health (Rodó *et al.,* 2024). Dust storms have been implicated in the outbreak of coccidioidomycosis (Valley fever; Pappagianis and Einstein, 1978) and meningococcal meningitis (*Neisseria meningitidis;* Maki *et al.,* 2022), while Spain and Iran have had instances of tularemia attributed to the inhalation of airborne environmental microbes entrained within the ambient environment (Zargar *et al.,* 2015). Biomass burned in wildfires is known to harbor major human respiratory pathogens and aeroallergens including *Cryptococcus gattii* (found in decayed trees) and a variety of molds found in decaying organic matter (*Aspergillus, Alternaria, Cladosporium, Mucor,* and *Penicillium* species; Figure 8.5). The most abundant belong to the phyla Ascomycota ("sac fungi" including morels, truffles, yeasts, mildews, and molds) and Basidiomycota ("higher fungi" including agarics, puffballs, rusts, and mirror yeasts). Specifically, the classes Dothideomycetes and Eurotiomycetes from Ascomycota and Agaricomycetes and Ustilaginomycetes from Basidiomycota appear the most frequently in smoke samples (Kobziar *et al.,* 2018; Kobziar *et al.,* 2022). It is important to note that not all fungi are harmful or toxic; indeed, most are beneficial, playing essential roles in maintaining ecosystem and human health. Nonetheless, fungal spores dispersed by smoke can adversely impact human health, primarily through acting as particulate matter in the lungs, triggering allergic reactions, exacerbating asthma, and imparting mycotoxins, which are linked to gastrointestinal issues, immune suppression, and cancer.

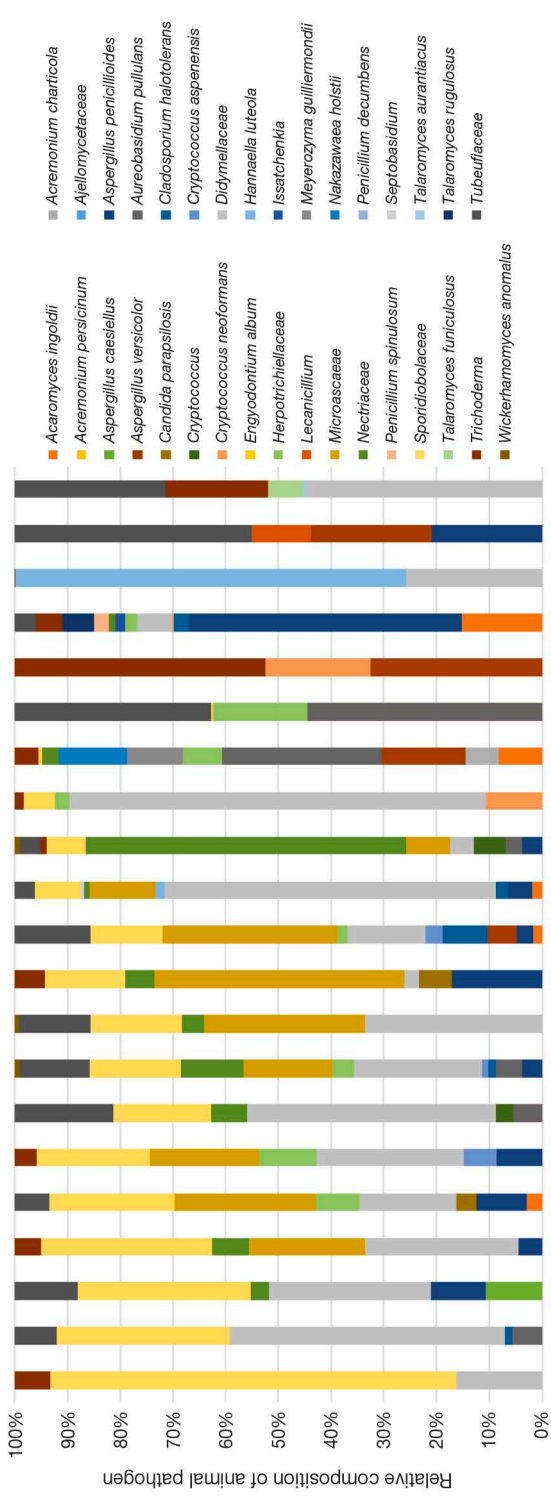

Figure 8.5. ITS rRNA sequencing amplicon sequence variant taxonomic assignments for fungi in smoke samples from longleaf pine forests in Florida, USA, identified as human/animal pathogens using FUNGuild (https://github.com/UMNFuN/FUNGuild). (Kobziar, Bonfantine and Lampman, *unpublished data*).

Significant knowledge gaps remain in predicting which fungal taxa are present in smoke from biomass fires. Although these bioaerosols contribute to human illnesses, little is known about their role in disease epidemiology. Table 8.1 emphasizes pathogenic fungi potentially transported in smoke.

Table 8.1. Genera of pathogenic fungi with member species either found or considered likely to be found in smoke. Fungi, which include yeasts, molds, and mushrooms, play a crucial role in decomposing organic matter, recycling nutrients in ecosystems, and maintaining soil health. While predominantly found in soil and vegetation, fungi occupy just about every habitat on Earth, including smoke (Fox *et al.,* 2022).

Genus	Class	Location if found in smoke	Description
Aspergillus	Eurotiomycetes	*Utah, Florida, California, Kansas*	Among the fungi found in smoke, *Aspergillus* is one of the most well-known and potentially harmful. *A. penicillioides* and *A. fumigatus* have been directly sampled in smoke (Kobziar *et al.,* 2022) and are associated with allergic rhinitis and asthma. Inhaled *Aspergillus* spores can also lead to pulmonary aspergillosis, a lung infection that can be severe, especially in immunocompromised individuals.
Cladophialohora	Eurotiomycetes	*Utah*	Known for their black pigmentation and filamentous growth, *Cladophialophora* species have been found in smoke from biomass fires (Kobziar *et al.,* 2022).
Coccidioides	Eurotiomycetes	n/a	Found primarily in arid and semi-arid soils of the southwestern United States, Mexico, and South America, *Coccidioides* species are responsible for coccidiomycosis, or Valley fever. To our knowledge, *Coccidioides* spores have not been isolated from smoke; however, hospital admissions within major cities not endemic for *Coccidioides* were elevated in the month following exposure to smoke from wildfires (Mulliken *et al.,* 2023).
Penicillium	Eurotiomycetes	*Utah, Florida, New Mexico, California, Idaho, Kansas*	*Penicillium* species, such as *P. lagena* (a non-pathogenic fungi found around mycorrhizal roots) have been sampled in smoke (Kobziar *et al.,* 2018). While this species is harmless, others, like *P. brevicompactum*, can produce mycotoxins such as mycophenolic acid, which can cause respiratory irritation, allergic reactions, and immune system suppression (Bentley, 2000).

Genus	Class	Location if found in smoke	Description
Alternaria	Dothideomycetes	*California, Kansas, Florida*	*Alternaria* species are also found in smoke (Kobziar *et al.,* 2022) and are known to produce various mycotoxins. Moreover, *Alternaria* species infect various crops, fruits, and vegetables (Meena and Samal, 2019).
Cladosporium	Dothideomycetes	*Utah, Florida, California, Kansas*	*Cladosporium* species are widespread in the environment and are frequently found in both air and smoke (Kobziar *et al.,* 2022). While they do not produce mycotoxins, their spores can cause allergic reactions and respiratory irritation in sensitive individuals.
Ochroconis	Dothideomycetes	*Kansas, Utah*	Commonly found in soil and decaying plants, *Ochroconis* species have been discovered in smoke (Kobziar *et al.,* 2022). *Ochroconis* infections are uncommon but can lead to phaeohyphomycosis, a rare fungal infection that manifests as skin lesions, subcutaneous nodules, or systemic infections, affecting the lungs, central nervous system, or other organs (Meriden *et al.,* 2012)
Candida	Saccharomycetes	*Kansas, California*	A genus that includes various yeasts, *Candida* species are commonly found as part of a healthy human microbiota on the skin, mucous membranes, and gastrointestinal tract. Infections, especially from *C. albicans,* may arise in immunocompromised individuals with symptoms ranging from superficial rashes to more severe systemic infections, such as invasive candidiasis from *C. auris*. *Candida* species have been found in smoke (Kobziar *et al.,* 2022).
Ustilago	Ustilaginomycetes	*Florida*	Known as smut fungi, *Ustilago* species are plant pathogens that primarily infect grasses and cereal crops, such as corn, wheat, and barley. Known to occur in smoke (Kobziar *et al.,* 2022), *U. hordei* has been associated with infertility and still births in farm animals (Constable *et al*., 2017).

Surprisingly, even critical reviews of human health consequences of wildfire smoke (Kobziar and Thompson, 2020) fail to address the microbial element. Knowledge of which microbes are transported, how far, and in what concentration could provide explanatory mechanisms in support of epidemiological patterns (Hauser *et al.,* 2021).

Although numerous fungal pathogens have been identified in smoke samples, whether other airborne pathogens such as *Coccidioides* spp., also found in the soils of fire-prone ecosystems, are aerosolized and transported by smoke plumes is presently unknown. Current hypotheses for host jumps from natural reservoirs to clinical infection centers in human populations do not address this potential pathway and have been generally much less parsimonious, relying on secondary hosts.

Although the studies documenting the microbial content of particulate emissions from wildland fires are limited, the research suggests that fire has the potential to mobilize agents causing invasive fungal infections (Kobziar and Thompson, 2020). For example, in studying fine mineral particles in airborne dust, the fungal organism *Coccidioides*, which is responsible for Valley fever, was shown to be associated with PM and dust in air (Kollath *et al.,* 2022; Weaver *et al.,* 2022, 2025). More compellingly, Mulliken *et al.* (2023) recently documented a 20% increase in Valley fever (coccidioidomycosis) hospital admissions within major cities not located in the endemic region in the one to three months following wildfire smoke exposure in California. Despite being an inhalable pathogen, airborne spores of this organism have been difficult to detect in air or in dust settling out of the atmosphere (Wagner *et al.,* 2023), suggesting that improved methods for atmospheric sampling are needed (Radosevich *et al.,* 2024).

Smoke's microbial aerosols may have macroscopic impacts by acting as a vector for pathogens of flora and fauna. Examples abound of tree species being decimated or even driven to extinction due to microbial pathogens, such as American chestnut blight (Rigling and Prospero, 2018), oak wilt (Wilson, 2001), sudden oak death (Rizzo and Garbelotto, 2003), thousand cankers disease (Daniels *et al.,* 2016), and white pine blister rust (Geils *et al.,* 2010). Similarly, pathogenic bioaerosols have historically wreaked havoc on agricultural crops, which due to the limited genetic diversity of most modern staples are at greater risk than their wild counterparts (Brown and Hovmøller, 2002). Smoke can disperse such pathogens to previously undisturbed regions lacking ecological resistance, with potential consequences to the ecosystem and agricultural products alike (Schmale and Ross, 2015).

⏩ Conclusion: The future looks…smoky

In many parts of the world, one or more of the following factors are increasing: Fire frequency, area burned in wildfire, or fire severity. Each of these factors leads to increased smoke production and transport. Smoke can travel hundreds to thousands of kilometers from its source (Colarco *et al.,* 2004; Cottle *et al.,* 2014; Hung *et al.,* 2020), carrying a diverse array of bioaerosols (Mims and Mims, 2004), but microbial survival over these distances is yet to be explicitly tested. In addition, the various repercussions of this transport are characterized by many unknowns. Overall, wildland fire dispersal of bioaerosols reveals a complex relationship among fire ecology, microbiology, and atmospheric sciences (Kobziar *et al.,* 2018), underscoring the need for further research to understand its implications for ecological resilience, infectious disease epidemiology, and biodiversity. For a young science, pyroaerobiology has made significant progress in proving basic principles. Continued global exploration of this phenomenon will deepen understanding across spatial and temporal scales and will inform a diversity of related sciences.

Literature cited

Alempic J.-M., *et al.*, 2023. An update on Eukaryotic viruses revived from ancient permafrost. *Viruses,* 15, 564. https://doi.org/10.3390/v15020564

Almeida E., *et al.*, 2018. The influence of meteorological parameters on *Alternaria* and *Cladosporium* fungal spore concentrations in Beja (Southern Portugal): Preliminary results. *Aerobiologia,* 34, 219-226. https://doi.org/10.1007/s10453-018-9508-8

Andreae M.O., 2019. Emission of trace gases and aerosols from biomass burning – an updated assessment. *Atmos. Chem. Phys.,* 19, 8523-8546. https://doi.org/10.5194/acp-19-8523-2019

Archer S.D.J., *et al.*, 2019. Airborne microbial transport limitation to isolated Antarctic soil habitats. *Nat. Microbiol.*, 4, 925-932. https://doi.org/10.1038/s41564-019-0370-4

Ardyna M., *et al.*, 2022. Wildfire aerosol deposition likely amplified a summertime Arctic phytoplankton bloom. *Communications Earth & Environment*, 3, 1-8. https://doi.org/10.1038/s43247-022-00511-9

Aubry-Wake C., *et al.*, 2022. Fire and ice: The impact of wildfire-affected albedo and irradiance on glacier melt. *Earth's Future*, 10, e2022EF002685. https://doi.org/10.1029/2022EF002685

Aurell J., *et al.*, 2015. Emissions from southeastern U.S. Grasslands and pine savannas: Comparison of aerial and ground field measurements with laboratory burns. *Atmos. Environ.*, 111, 170-178. https://doi.org/10.1016/j.atmosenv.2015.03.001

Aurell J., *et al.*, 2021. Wildland fire emission sampling at Fishlake National Forest, Utah using an unmanned aircraft system. *Atmos. Environ.*, 247, 118193. https://doi.org/10.1016/j.atmosenv.2021.118193

Aylor D.E., *et al.*, 2011. Tracking the potato late blight pathogen in the atmosphere using unmanned aerial vehicles and Lagrangian modeling. *Agric. For. Meteorol.*, 151, 251-260. https://doi.org/10.1016/j.agrformet.2010.10.013

Barberán A., *et al.*, 2015. Continental-scale distributions of dust-associated bacteria and fungi. *Proc. Natl Acad. Sci. USA,* 112, 5756-5761. https://doi.org/10.1073/pnas.1420815112

Barkley A.E., *et al.*, 2019. African biomass burning is a substantial source of phosphorus deposition to the Amazon, Tropical Atlantic Ocean, and Southern Ocean. *Proc. Natl Acad. Sci. USA,* 116, 16216-16221. https://doi.org/10.1073/pnas.1906091116

Barry K.R., *et al.*, 2021. Observations of ice nucleating particles in the free troposphere from western US wildfires. *J. Geophys. Res.: Atmospheres*, 126, e2020JD033752. https://doi.org/10.1029/2020JD033752

Bauer H., *et al.*, 2003. Airborne bacteria as cloud condensation nuclei. *J. Geophys. Res.: Atmospheres*, 108, 4658. https://doi.org/10.1029/2003JD003545

Behzad H., *et al.*, 2015. Challenges and opportunities of airborne metagenomics. *Genome Biol. Evol.*, 7, 1216-1226. https://doi.org/10.1093/gbe/evv064

Bentley R., 2000. Mycophenolic acid: A one hundred year odyssey from antibiotic to immunosuppressant. *Chem. Rev.*, 100, 3801-3826. https://doi.org/10.1021/cr990097b

Bonfantine K., *et al.*, 2024. Evidence for wildland fire smoke transport of microbes from terrestrial sources to the atmosphere and back. *J. Geophys. Res.: Biogeosciences*, 129, e2024JG008236. https://doi.org/10.1029/2024JG008236

Boreson J., *et al.*, 2004. Correlating bioaerosol load with $PM_{2.5}$ and PM_{10}cf concentrations: A comparison between natural desert and urban-fringe aerosols. *Atmos. Environ.*, 38, 6029-6041. https://doi.org/10.1016/j.atmosenv.2004.06.040

Bormann B.T., *et al.*, 2008. Intense forest wildfire sharply reduces mineral soil C and N: The first direct evidence. *Canadian J. Forest Res.*, 38, 2771-2783. https://doi.org/10.1139/X08-136

Bowers J.R., *et al.*, 2019. Direct detection of Coccidioides from Arizona soils using CocciENV, a highly sensitive and specific real-time PCR assay. *Medical Mycology*, 57, 246-255. https://doi.org/10.1093/mmy/myy007

Brown J.K.M., Hovmøller M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science*, 297, 537-541. https://doi.org/10.1126/science.1072678

Busse M.D., *et al.*, 2013. Soil heating during burning of forest slash piles and wood piles. *Int. J. Wildl. Fire*, 22, 786. https://doi.org/10.1071/WF12179

Christner B.C., *et al.*, 2008. Geographic, seasonal, and precipitation chemistry influence on the abundance and activity of biological ice nucleators in rain and snow. *Proc. Natl Acad. Sci. USA,* 105, 18854-18859. https://doi.org/10.1073/pnas.0809816105

Colarco P.R., *et al.*, 2004. Transport of smoke from Canadian forest fires to the surface near Washington D.C.: Injection height, entrainment, and optical properties. *J. Geophys. Res.: Atmospheres*, 109. https://doi.org/10.1029/2003JD004248

Constable P.D., *et al*., 2017. Diseases primarily affecting the reproductive system. *In: Veterinary medicine (Eleventh Edition)*, W.B. Saunders, 1758-1829. https://doi.org/10.1016/B978-0-7020-5246-0.00018-8

Cottle P., *et al.*, 2014. Long-range transport of Siberian wildfire smoke to British Columbia: Lidar observations and air quality impacts. *Atmos. Environ.*, 90, 71-77. https://doi.org/10.1016/j.atmosenv.2014.03.005

Daniels D.A., *et al.*, 2016. Thousand cankers disease complex: A forest health issue that threatens *Juglans* species across the U.S. *Forests*, 7. https://doi.org/10.3390/f7110260

DeMott P.J., *et al.*, 2010. Predicting global atmospheric ice nuclei distributions and their impacts on climate. *Proc. Natl Acad. Sci. USA,* 107, 11217-11222. https://doi.org/10.1073/pnas.0910818107

Dirksen R.J., *et al.*, 2009. An aerosol boomerang: Rapid around-the-world transport of smoke from the December 2006 Australian Forest fires observed from space. *J. Geophys. Res.: Atmospheres*, 114. https://doi.org/10.1029/2009JD012360

Earl S.R., Blinn D.W., 2003. Effects of wildfire ash on water chemistry and biota in South-Western U.S.A. streams. *Freshwater Biology*, 48, 1015-1030. https://doi.org/10.1046/j.1365-2427.2003.01066.x

Ellington A.J., *et al.*, 2024. Dispersal of microbes from grassland fire smoke to soils. *ISME J.*, wrae203. https://doi.org/10.1093/ismejo/wrae203

Evans J.S., *et al.*, 2021. Evidence of smoke from wildland fire in surface water of an unburned watershed. *Water Resour. Res.*, 57, e2021WR030069. https://doi.org/10.1029/2021WR030069

Fierer N., *et al.*, 2010. Changes through time: Integrating microorganisms into the study of succession. *Res. Microbiol.*, 161, 635-642. https://doi.org/10.1016/j.resmic.2010.06.002

Fox S., *et al.*, 2022. Fire as a driver of fungal diversity – A synthesis of current knowledge. *Mycologia*, 114, 215-241. https://doi.org/10.1080/00275514.2021.2024422

Frohlich-Nowoisky J., *et al.*, 2009. High diversity of fungi in air particulate matter. *Proc. Natl Acad. Sci. USA,* 106, 12814-12819. https://doi.org/10.1073/pnas.0811003106

Geils B.W., *et al.*, 2010. White pines, Ribes, and blister rust: A review and synthesis. *Forest Pathology*, 40, 147-185. https://doi.org/10.1111/j.1439-0329.2010.00654.x

Glassman S.I., *et al.*, 2016. Ectomycorrhizal fungal spore bank recovery after a severe forest fire: Some like it hot. *ISME J.*, 10, 1228-1239. https://doi.org/10.1038/ismej.2015.182

Griffin D.W. 2007. Atmospheric movement of microorganisms in clouds of desert dust and implications for human health. *Clin. Microbiol. Rev.*, 20, 459-477. https://doi.org/10.1128/CMR.00039-06

Harris J., 2009. Soil microbial communities and restoration ecology: Facilitators or followers? *Science*, 325, 573-574. https://doi.org/10.1126/science.1172975

Hauser N., *et al.*, 2021. Climate change and infections on the move in North America. *Infect. Drug Resist.*, 14, 5711-5723. https://doi.org/10.2147/IDR.S305077

Hirst J.M., 1952. An automatic volumetric spore trap. *Ann. Appl. Biol.*, 39, 257-265. https://doi.org/10.1111/j.1744-7348.1952.tb00904.x

Hung W.-T., *et al.*, 2020. The impacts of transported wildfire smoke aerosols on surface air quality in New York State: A case study in summer 2018. *Atmos. Environ.*, 227, 117415. https://doi.org/10.1016/j.atmosenv.2020.117415

Inci G., *et al.*, 2017. Langevin dynamics simulation of transport and aggregation of soot nano-particles in turbulent flows. *Flow, Turbulence and Combustion*, 98, 1065-1085. https://doi.org/10.1007/s10494-016-9797-3

Jones M.W., *et al.*, 2022. Global and regional trends and drivers of fire under climate change. *Rev. Geophys.*, 60, e2020RG000726. https://doi.org/10.1029/2020RG000726

Kobziar L.N., *et al.*, 2018. Pyroaerobiology: The aerosolization and transport of viable microbial life by wildland fire. *Ecosphere*, 9, e02507. https://doi.org/10.1002/ecs2.2507

Kobziar L.N., *et al.*, 2019. Accessing the life in smoke: A new application of Unmanned Aircraft Systems (UAS) to sample wildland fire bioaerosol emissions and their environment. *Fire,* 2, 56. https://doi.org/10.3390/fire2040056

Kobziar L.N., Thompson G.R., 2020. Wildfire smoke, a potential infectious agent. *Science*, 370, 1408-1410. https://doi.org/10.1126/science.abe8116

Kobziar L.N., *et al.*, 2022. Wildland fire smoke alters the composition, diversity, and potential atmospheric function of microbial life in the aerobiome. *ISME Communications*, 2, 1-9. https://doi.org/10.1038/s43705-022-00089-5

Kobziar L.N., *et al.*, 2024a. Principles of fire ecology. *Fire Ecology*, 20, 39. https://doi.org/10.1186/s42408-024-00272-0

Kobziar L.N., *et al.*, 2024b. Bacterial emission factors: A foundation for the terrestrial-atmospheric modeling of bacteria aerosolized by wildland fires. *Environ. Sci. Technol.*, 58, 2413-2422. https://doi.org/10.1021/acs.est.3c05142

Kollath D.R., *et al.*, 2022. PM_{10} and other climatic variables are important predictors of seasonal variability of Coccidioidomycosis in Arizona. *Microbiology Spectrum*, 10, e0148321. https://doi.org/10.1128/spectrum.01483-21

Koplitz S.N., *et al.*, 2021. The contribution of wildland fire emissions to deposition in the US: Implications for tree growth and survival in the Northwest. *Environ. Res. Lett.*, 16, 024028. https://doi.org/10.1088/1748-9326/abd26e

Kreye J.K., *et al.*, 2020. Long-duration soil heating resulting from forest floor duff smoldering in longleaf pine ecosystems. *Forest Science*, 66, 291-303. https://doi.org/10.1093/forsci/fxz089

Lappan R., *et al.*, 2024. The atmosphere: A transport medium or an active microbial ecosystem? *ISME J.*, 18, wrae092. https://doi.org/10.1093/ismejo/wrae092

Maki T., *et al.*, 2022. Long-range transport of airborne bacteria over East Asia: Asian dust events carry potentially nontuberculous *Mycobacterium* populations. *Environ. Int.*, 168, 107471. https://doi.org/10.1016/j.envint.2022.107471

McCluskey C.S., *et al.*, 2014. Characteristics of atmospheric ice nucleating particles associated with biomass burning in the US: Prescribed burns and wildfires. *J. Geophys. Res.: Atmospheres*, 119, 10458-10470. https://doi.org/10.1002/2014JD021980

Meena M., Samal S., 2019. Alternaria host-specific (HSTs) toxins: An overview of chemical characterization, target sites, regulation and their toxic effects. *Toxicol. Rep.*, 6, 745-758. https://doi.org/10.1016/j.toxrep.2019.06.021

Meriden Z., *et al*., 2012. *Ochroconis gallopava* infection in a patient with chronic granulomatous disease: Case report and review of the literature. *Med. Mycol.*, 50, 883-889. https://doi.org/10.3109/13693786.2012.681075

Miaow K., *et al.*, 2021. Identifying optimal bioinformatics protocols for aerosol microbial community data. *Peer J.*, 9, e12065. https://doi.org/10.7717/peerj.12065

Michaud L., *et al.*, 2014. Snow surface microbiome on the High Antarctic Plateau (DOME C). *PLoS ONE*, 9, e104505. https://doi.org/10.1371/journal.pone.0104505

Mims S.A., Mims F.M., 2004. Fungal spores are transported long distances in smoke from biomass fires. *Atmos. Environ.*, 38, 651-655. https://doi.org/10.1016/j.atmosenv.2003.10.043

Mirskaya E., Agranovski I.E., 2020. Generation of viable bacterial and fungal aerosols during biomass combustion. *Atmosphere*, 11, 313. https://doi.org/10.3390/atmos11030313

Moore R.A., *et al.*, 2020. Wildland fire as an atmospheric source of viable microbial aerosols and biological ice nucleating particles. *ISME J.*, 15 (2), 461-472. https://doi.org/10.1038/s41396-020-00788-8

Morris C.E., *et al.*, 2008. The life history of the plant pathogen *Pseudomonas syringae* is linked to the water cycle. *ISME J.*, 2, 321-334. https://doi.org/10.1038/ismej.2007.113

Morris C.E., *et al.*, 2013. Urediospores of rust fungi are ice nucleation active at > −10°C and harbor ice nucleation active bacteria. *Atmos. Phys. Chem.* 13, 4223-4233. https://doi.org/10.5194/acp-13-4223-2013

Morris C.E., *et al.*, 2014. Bioprecipitation: A feedback cycle linking Earth history, ecosystem dynamics and land use through biological ice nucleators in the atmosphere. *Global Change Biology*, 20, 341-351. https://doi.org/10.1111/gcb.12447

Mulliken J.S., *et al.*, 2023. Risk of systemic fungal infections after exposure to wildfires: A population-based, retrospective study in California. *Lancet Planet. Health*, 7, e381-e386. https://doi.org/10.1016/S2542-5196(23)00046-3

Nelson K.N., *et al.*, 2019. A multipollutant smoke emissions sensing and sampling instrument package for unmanned aircraft systems: Development and testing. *Fire*, 2 (2), 32. https://doi.org/10.3390/fire2020032

Olson N.E., *et al.*, 2023. Wildfires in the western United States are mobilizing $PM_{2.5}$-associated nutrients and may be contributing to downwind cyanobacteria blooms. *Environmental Science: Processes & Impacts*, 25, 1049-1066. https://doi.org/10.1039/D3EM00042G

Pappagianis D., Einstein H., 1978. Tempest from Tehachapi takes toll or Coccidioides conveyed aloft and afar. *West. J. Med.*, 129, 527-530.

Pearce D.A., *et al.*, 2016. Aerobiology over Antarctica – A new initiative for atmospheric ecology. *Front. Microbiol.*, 7. https://doi.org/10.3389/fmicb.2016.00016

Perron M.M.G., *et al.*, 2022. Trace elements and nutrients in wildfire plumes to the southeast of Australia. *Atmospheric Res.*, 270, 106084. https://doi.org/10.1016/j.atmosres.2022.106084

Pingree M.R.A., Kobziar L.N., 2019. The myth of the biological threshold: A review of biological responses to soil heating associated with wildland fire. *Forest Ecology and Management*, 432, 1022-1029. https://doi.org/10.1016/j.foreco.2018.10.032

Pisaric M.F.J., 2002. Long-distance transport of terrestrial plant material by convection resulting from forest fires. *Journal of Paleolimnology*, 28, 349-354. https://doi.org/10.1023/A:1021630017078

Pretorius I., *et al.*, 2023. In the wind: Invasive species travel along predictable atmospheric pathways. *Ecol. Appl.*, 33, e2806. https://doi.org/10.1002/eap.2806

Prichard S.J., *et al.*, 2014. Evaluation of the CONSUME and FOFEM fuel consumption models in pine and mixed hardwood forests of the eastern United States. *Canadian Journal of Forest Research*, 44, 784-795. https://doi.org/10.1139/cjfr-2013-0499

Prichard S., *et al.*, 2020. Wildland fire emission factors in North America: Synthesis of existing data, measurement needs and management applications. *International Journal of Wildland Fire*, 29 (2), 132-147. https://doi.org/10.1071/WF19066

Radosevich M.T., *et al.*, 2024. Detection of airborne *Coccidioides* spores using lightweight portable air samplers affixed to uncrewed aircraft systems in California's Central Valley. *bioRxiv*, 2024.10.28.620741. https://doi.org/10.1101/2024.10.28.620741

Rajput P., *et al.*, 2017. One year record of bioaerosols and particles concentration in Indo-Gangetic Plain: Implications of biomass burning emissions to high-level of endotoxin exposure. *Environmental Pollution*, 224, 98-106. https://doi.org/10.1016/j.envpol.2017.01.045

Reichman J.R., *et al.*, 2021. Focused microbiome shifts in reconstructed wetlands correlated with elevated copper concentrations originating from micronized copper azole-treated wood. *Environmental Toxicology and Chemistry*, 40, 3351-3368. https://doi.org/10.1002/etc.5219

Reinhardt E.D., *et al.*, 1997. First Order Fire Effects Model: FOFEM 4.0, User's guide. Gen. Tech. Rep. INT-GTR-344. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, 65 p. https://doi.org/10.2737/INT-GTR-344

Rigling D., Prospero S., 2018. *Cryphonectria parasitica*, the causal agent of chestnut blight: Invasion history, population biology and disease control. *Molecular Plant Pathology*, 19, 7-20. https://doi.org/10.1111/mpp.12542

Rizzo D.M., Garbelotto M., 2003. Sudden oak death: Endangering California and Oregon forest ecosystems. *Front. Ecol. Environ.*, 1, 197-204. https://doi.org/10.1890/1540-9295(2003)001[0197:SODECA]2.0.CO;2

Rodó X., *et al.*, 2024. Microbial richness and air chemistry in aerosols above the PBL confirm 2,000-km long-distance transport of potential human pathogens. *Proc. Natl Acad. Sci. USA,* 121, e2404191121. https://doi.org/10.1073/pnas.2404191121

Schmale D.G., Ross S.D., 2015. Highways in the sky: Scales of atmospheric transport of plant pathogens. *Annu. Rev. Phytopathol.*, 53, 591-611. https://doi.org/10.1146/annurev-phyto-080614-115942

Schmale D.G., *et al.*, 2012. Isolates of *Fusarium graminearum* collected 40–320 meters above ground level cause Fusarium head blight in wheat and produce trichothecene mycotoxins. *Aerobiologia*, 28, 1-11. https://doi.org/10.1007/s10453-011-9206-2

Simoneit B.R.T., 2002. Biomass burning—a review of organic tracers for smoke from incomplete combustion. *Applied Geochemistry*, 17, 129-162. https://doi.org/10.1016/S0883-2927(01)00061-0

Smith D.J., *et al.*, 2011. Microbial survival in the stratosphere and implications for global dispersal. *Aerobiologia*, 27, 319-332. https://doi.org/10.1007/s10453-011-9203-5

Spencer C.N., Hauer F.R., 1991. Phosphorus and nitrogen dynamics in streams during a wildfire. *Journal of the North American Benthological Society*, 10, 24-30. https://doi.org/10.2307/1467761

Spracklen D.V., Heald C.L., 2014. The contribution of fungal spores and bacteria to regional and global aerosol number and ice nucleation immersion freezing rates. *Atmos. Chem. Phys.*, 14, 9051-9059. https://doi.org/10.5194/acp-14-9051-2014

Stein A.F., *et al.*, 2015. NOAA's HYSPLIT atmospheric transport and dispersion modeling system. *Bull. Am. Meteorol. Soc.*, 96, 2059-2077. https://doi.org/10.1175/BAMS-D-14-00110.1

Stoddard J.L., *et al.*, 2016. Continental-scale increase in lake and stream phosphorus: Are oligtrophic systems disappearing in the United States? *Environ. Sci. Technol.*, 50, 3409-3415. https://doi.org/10.1021/acs.est.5b05950

Tang W., *et al.*, 2021. Widespread phytoplankton blooms triggered by 2019-2020 Australian wildfires. *Nature*, 597, 370-375. https://doi.org/10.1038/s41586-021-03805-8

Tencé F., *et al.*, 2022. Australian black summer smoke observed by lidar at the French Antarctic station Dumont d'Urville. *J. Geophys. Res.: Atmospheres*, 127, e2021JD035349. https://doi.org/10.1029/2021JD035349

Tyagi P., *et al.*, 2016. Impact of biomass burning on soil microorganisms and plant metabolites: A view from molecular distributions of atmospheric hydroxy fatty acids over Mount Tai. *J. Geophys. Res.: Biogeosciences*, 121, 2684-2699. https://doi.org/10.1002/2016JG003324

Villa T.F., *et al.*, 2016. An overview of small unmanned aerial vehicles for air quality measurements: Present applications and future prospectives. *Sensors*, 16 (7), 1072. https://doi.org/10.3390/s16071072

Wagner R., *et al.*, 2023. Coccidioides undetected in soils from agricultural land and uncorrelated with time or the greater soil fungal community on undeveloped land. *PLOS Pathogens*, 19, 1-29. https://doi.org/10.1371/journal.ppat.1011391

Wang Y., *et al.*, 2022. Australian fire nourishes ocean phytoplankton bloom. *Sci. Tot. Environ*, 807, 150775. https://doi.org/10.1016/j.scitotenv.2021.150775

Weaver A.K., *et al.*, 2022. Environmental factors influencing COVID-19 incidence and severity. *Ann. Rev. Public Health*, 43, 271-291. https://doi.org/10.1146/annurev-publhealth-052120-101420

Weaver A.K., *et al.*, 2025. Estimating the exposure-response relationship between fine mineral dust concentration and coccidioidomycosis incidence using speciated particulate matter data: A longitudinal surveillance study. *Environ. Health Perspect.*, 133, 17003. https://doi.org/10.1289/EHP13875

Williams C.L., *et al.*, 2017. Biomass compositional analysis for conversion to renewable fuels and chemicals. *IntechOpen*. https://www.intechopen.com/chapters/52751

Wilson A.D., 2001. Oak wilt: A potential threat to southern and western oak forests. *Journal of Forestry*, 99, 4-11. https://doi.org/10.1093/jof/99.5.4

Woo C., Yamamoto N., 2020. Falling bacterial communities from the atmosphere. *Environ. Microbiome*, 15, 22. https://doi.org/10.1186/s40793-020-00369-4

Yang Y., *et al.*, 2012. Observation of elevated fungal tracers due to biomass burning in the Sichuan Basin at Chengdu City, China. *Sci. Tot. Environ*, 431, 68-77. https://doi.org/10.1016/j.scitotenv.2012.05.033

Yokelson R.J., *et al.*, 1996. Open-path Fourier transform infrared studies of large-scale laboratory biomass fires. *JGR Atmospheres*, 101(D15), 21067-21080. https://doi.org/10.1029/96JD01800

Yue S., *et al.* (2025). Mass deposition of microbes from wildfire smoke to the sea surface microlayer. *Limnology and Oceanography*, 70 (6), 1770-81. https://doi.org/10.1002/lno.70078

Zargar A., *et al.*, 2015. Tularemia, a re-emerging infectious disease in Iran and neighboring countries. *Epidemiology and Health*, 37, e2015011. https://doi.org/10.4178/epih/e2015011

Zhang T., *et al.*, 2008. Identification and estimation of the biomass burning contribution to Beijing aerosol using levoglucosan as a molecular marker. *Atmos. Environ.*, 42, 7013-7021. https://doi.org/10.1016/j.atmosenv.2008.04.050

Zhong Y., *et al.*, 2018. Decreased occurrence of carbon cycle functions in microbial communities along with long-term secondary succession. *Soil Biol. Biochem.*, 123, 207-217. https://doi.org/10.1016/j.soilbio.2018.05.017

Zhou Y., *et al.*, 2022. Fire decreases soil enzyme activities and reorganizes microbially mediated nutrient cycles: A meta-analysis. *Ecology*, 103, e3807. https://doi.org/10.1002/ecy.3807

Zhu Z., *et al.*, 2024. Effects of forest fire smoke deposition on soil physico-chemical properties and bacterial community. *Sci. Tot. Environ*, 909, 168592. https://doi.org/10.1016/j.scitotenv.2023.168592

Chapter 9

More than wings: Long-distance dissemination of insects in the atmosphere

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Insect dissemination across long distances has captivated human curiosity for centuries. Historical references highlight, for example, the significant impact of migratory swarms, such as those of the desert locust *Schistocerca gregaria* in Africa, western Asia, and India, whose devastating effects on agriculture have been known since antiquity (Akhter *et al.*, 2023; Wang *et al.*, 2014). While migration is observed across various animal taxa, insects notably dominate this phenomenon because of their abundance and their presence in almost every region of the globe. For example, recent radar data indicate that approximately 9.3 trillion nocturnal insect migrants disseminate annually over eastern China (Huang *et al.*, 2024). Additionally, in northern Australia and Africa respectively, 2 billion Bogong moths (*Agrotis infusa*) and significant swarms of desert locusts (*Schistocerca gregaria*), that can reach 50 million per square kilometer, further illustrate the magnitude of insect migration (Satterfield *et al.*, 2020).

Insects also fascinate due to their ability to travel great distances. Well-documented examples include the painted lady butterfly *Vanessa cardui*, which achieves an extraordinary multi-generational journey between Europe and Africa each year, with well characterized spring flights from the Maghreb to Europe and autumn migrations with hypothesized crossing of both the Mediterranean Sea and the Sahara Desert by migrants, implying the longest migratory flight recorded for a butterfly in a single generation (>4,000 km; Talavera and Vila, 2017). This species has thus become a model for the study of insect migration alongside the famous monarch butterfly *Danaus plexippus*, one of the most famous cases of insect round-trip migration, involving up to five generations between Canada and Mexico (Stefanescu *et al.*, 2013; Talavera and Vila, 2017; Reppert and De Roode, 2018; Talavera *et al.*, 2023). The globe skimmer dragonfly *Pantala flavescens* also exhibits one of the longest known insect migration, hypothesized to total between 14,000 and 18,000 km over four generations (Anderson, 2009), including a non-stop migration of 3,500 km or more across the western India Ocean from India to East Africa (and back). In comparison, for *Vanessa cardui*, a transoceanic crossing of at least 4,200 km from West Africa to South America has been documented (Suchan *et al.*, 2024). Similarly, the desert locust *Schistocerca gregaria* can migrate up to 5,000 km in northern Africa (Alerstam *et al.*, 2003).

However, these migrations are not merely fascinating natural phenomena, they have ecological and economic implications. Indeed, insect migrations play critical roles in ecosystems, providing beneficial services as well as causing detrimental effects, which can affect the biological balance within these ecosystems and even have consequences for human, animal and plant health (Chapman *et al.*, 2015; Reynolds *et al.*, 2017).

Despite being the most abundant and economically important terrestrial migrants (Chapman *et al.*, 2015), tracking insect movements remains challenging due to their small size, abundant populations, and ability to travel vast distances actively or passively via air currents (Osborne *et al.*, 2002; Chapman *et al.*, 2015). However, advances in tracking techniques, population genetics and dynamics studies, and modelling are gradually enhancing our understanding of insect dissemination, which is essential given the urgency to address the aforementioned impacts (Osborne *et al.*, 2002; Chapman *et al.*, 2015; Satterfield *et al.*, 2020).

Many authors previously laid the groundwork for insect flight via air masses, but they focused mostly on the physical processes involved, or only on the consequences of these flights, as well as covering mainly or only seasonal migrations, or certain types of insects (i.e., vectors, certain size categories or taxonomic groups, etc.) (Chapman *et al.*, 2015; Reynolds *et al.*, 2006, 2017; Satterfield *et al.*, 2020). This chapter aims to present an overview of the mechanisms of long-distance windborne insect dissemination, as well as the range of insect species disseminated in the atmosphere, with use of the terms migration, dispersal and dissemination as described in Box 9.1. The chapter also presents how dissemination is linked to the insect's biological traits by discussing their adaptation to dissemination and its consequences on their biology, ecology, evolution and ecosystems. By synthesizing current knowledge and presenting the most recent advances on the subject, we hope to provide insights that can aid in informing aerobiology, population ecology, pest and disease management, and conservation biology.

⏩ High-altitude dissemination of insects: Windborne dissemination and quasi-passive flight

Proof and range of insect presence and dissemination at high altitude

Evidence of long-distance dissemination of insects in the atmosphere is mostly indirect, typically gathered through ground level presence/absence records, breeding site locations, changes in seasonal distribution, population genetics studies or approximate flight directions (inferred by wind directions aligned with migration patterns). However, other biological or ecological studies like those on insect flight physiology, behaviour, ecology or phenology, can also be used to gain insight on insect flight and dissemination. Methods and tools for assessing wind-assisted dispersal of insects are reviewed in Chapter 11. For instance, the alignment of favourable winds, inferred from backtracking air trajectories, with the range expansion of the biting midge *Culicoides imicola* in continental France, as well as population genetics studies, suggest that this range expansion was probably due to rare wind-transport events from Corsica (Jacquet *et al.*, 2016).

Some other proofs are direct, including high-altitude sampling of insects in air masses (using nets attached to aircrafts, tethered balloons or parafoil kites), and

provide evidence of the presence of these insects in the troposphere. For example, small hemipteran-like aphids have been captured at high altitude in the atmosphere for a long time (Berry and Taylor, 1968; Loxdale *et al.*, 1993). More recently other hemipterans (i.e., psyllids such as *Cacopsylla melanoneura* and *C. affinis*) have also been captured at high altitude (200 m above ground) over England and above seas, far from land (Greenslade *et al.*, 2021). In northeast India and the Sahel, many species of mosquitoes (*Anopheles* spp., *Aedes* spp., *Mansonia* spp., and *Culex* spp.*)* were caught at heights of 40 to 290 m on long-distance windborne journeys in multiple studies, indicating that this method of dissemination is widespread across diverse genera and species (Florio *et al.*, 2020; Huestis *et al.*, 2019; Service, 1997; Yaro *et al.*, 2022). Other more recent technological advancements, such as Vertical-Looking (entomological) Radar (VLR), have enabled scientists to directly quantify insect movements beyond human perception. This technology has revealed that while low-altitude insect movements are spectacular, high-altitude movements (150–1,200 m) are even more substantial (Chapman *et al.*, 2011). Radar data have, for example, shown large-scale migrations of painted lady butterflies *V. cardui*, silver Y moths *Autographa gamma*, ladybirds *Coccinella septempunctata* and *Harmonia axyridis*, and hoverflies (e.g., *Episyrphus balteatus*, *Eupeodes corollae*) in the UK, with millions of individuals migrating each year (Jeffries *et al.*, 2013; Satterfield *et al.*, 2020; Stefanescu *et al.*, 2013; Wotton *et al.*, 2019).

Box 9.1. The language of movements: Defining migration, dispersal and dissemination

In this chapter, we will use the definitions by Dingle and colleagues (2007, 2014) based on Kennedy's (1985), where "migration" is mainly characterized by "persistent straightened-out movements undistracted by the cues indicating resources, and of longer duration than during station keeping or ranging/foraging". Migration is therefore defined as an individual-based behavioural phenomenon that has ecological and population-scale consequences. For many entomologists, this definition of migration is compatible with our modern understanding of the mode of action of natural selection (as acting on individuals and their genes) and it is agreed that it is best to consider migration behaviourally, thus making this definition the most widely accepted in articles on which we have based our review (Asplen, 2018; Chapman *et al.*, 2015; Dingle and Drake, 2007; Osborne *et al.*, 2002; Renault, 2020; Reynolds *et al.*, 2006, 2017). Following the definitions from the same authors, we consider "dispersal" as one-way movements leading to a displacement from the natal or breeding habitat to another breeding habitat, or an increase in distance between members of a population (i.e., intergenerational – spatial – movement) (Asplen, 2018; Clobert *et al.*, 2009; Osborne *et al.*, 2002; Renault, 2020). Contrary to migration, dispersal is better considered at the population scale, encompassing the ideas of the scattering of individuals, along with other phenomena of population redistribution (Dingle, 2014; Renault, 2020). Thus, dispersal is a potential (but not obligatory) outcome of migration, and conversely, not all dispersal events are migratory (Osborne *et al.*, 2002; Dingle, 2014; Asplen, 2018). In this chapter, since we are interested in all movements of insects in the atmosphere, whether it is considered migration and/or dispersal, we will also use the word "dissemination" as encompassing all movements of insects carried by the wind in the atmosphere.

Direct proofs also helped researchers to decipher characteristics of insect flights in the atmosphere such as altitudes, densities and sizes. For instance, insects have been detected at altitudes of up to 2 km above ground level under warm conditions, with occasional flights reaching 4-5 km altitude due to favourable atmospheric temperatures. This indicates that insects occupy the Planetary Boundary Layer (PBL, the lower, most turbulent atmospheric layer extending from 100 m to 2-3 km altitude), sometimes called the Atmospheric Boundary Layer (ABL), and the lower troposphere above it (Figure 9.1A; Reynolds *et al.*, 2017). For example, helicopter-mounted traps and VLR data showed that the highest density for species such as aphids and hoverflies is observed at altitudes <500 m and <300 m respectively, while for the brown planthopper *Nilaparvata lugens* it is between 1,500 m and 2,000 m (Dung, 1981; Isard *et al.*, 1990; Wotton *et al.*, 2019). Moreover, sampling efforts using aerial sampling have provided insights into the distribution of insects of different sizes at various altitudes. In the UK for example, insect size frequency distribution shows a peak for insects weighing 0.5-1 mg, primarily aphids, small flies (Diptera) and parasitoid wasps (Hymenoptera). Insects larger than 10 mg are significantly less common, with densities decreasing dramatically as size increases (Reynolds *et al.*, 2017).

Table 9.1 summarizes the diversity, range, and biological characteristics of insect taxa known to be dispersed by wind at high altitudes in the atmosphere. The table includes information on taxonomy, size/weight, and other traits relevant to their aerial dissemination. Both direct and indirect evidence of windborne transport were considered. Rather than aiming for exhaustiveness, this synthesis highlights the taxonomic and ecological breadth and range of wind-dispersed insects identified in our literature review.

How insects disseminate: Active and passive flights

Insects, being relatively small, often have low self-propelled flight speeds. Consequently, their foraging flight occurs primarily within their Flight Boundary Layer (FBL), the zone close to the ground where ambient wind speeds are lower than the insect's self-propelled flight speed, enabling them to control their direction and movements (Figure 9.1A; Chapman *et al.*, 2015; Gao *et al.*, 2020; Reynolds *et al.*, 2017; Taylor, 1974). Thus, some insects can engage in active migratory flight close to the Earth's surface. For instance, butterflies and dragonflies are typical examples of within-FBL migrating insects, in the sense that they undertake both short- and long-distance migrations within their FBL (Chapman *et al.,* 2010, 2015).

But overall, high-altitude windborne dissemination is more common than within the FBL. Indeed, many insects exploit wind currents for long-distance migration, and their dissemination is thus highly defined by winds (Table 9.1). We will discuss below in detail how insects can exert control over this phenomenon. These high-altitude aerial movements enable insects to colonize and exploit new habitats, sometimes covering considerable distances, going further and faster than would be possible by self-propelled flight alone (Reynolds *et al.*, 2006, 2017). For example, even small weak-flying insects such as psyllids and aphids (i.e., Hemiptera) can exploit wind currents for long-distance dispersal, sometimes travelling hundreds of kilometers (Greenslade *et al.*, 2021; Isard *et al.*, 1990; Strona *et al.*, 2020). As for the boll weevil *Anthonomus grandis*, another weak flier, historical data have documented dispersal events ranging

from 41 km to 272 km when aided by wind currents (Kim and Sappington, 2013). Furthermore, certain insects have the ability to continue their dissemination at night or resume flight on successive days (e.g., locusts), which enables them to travel even greater distances (Berry and Taylor, 1968; Reynolds *et al.*, 2017).

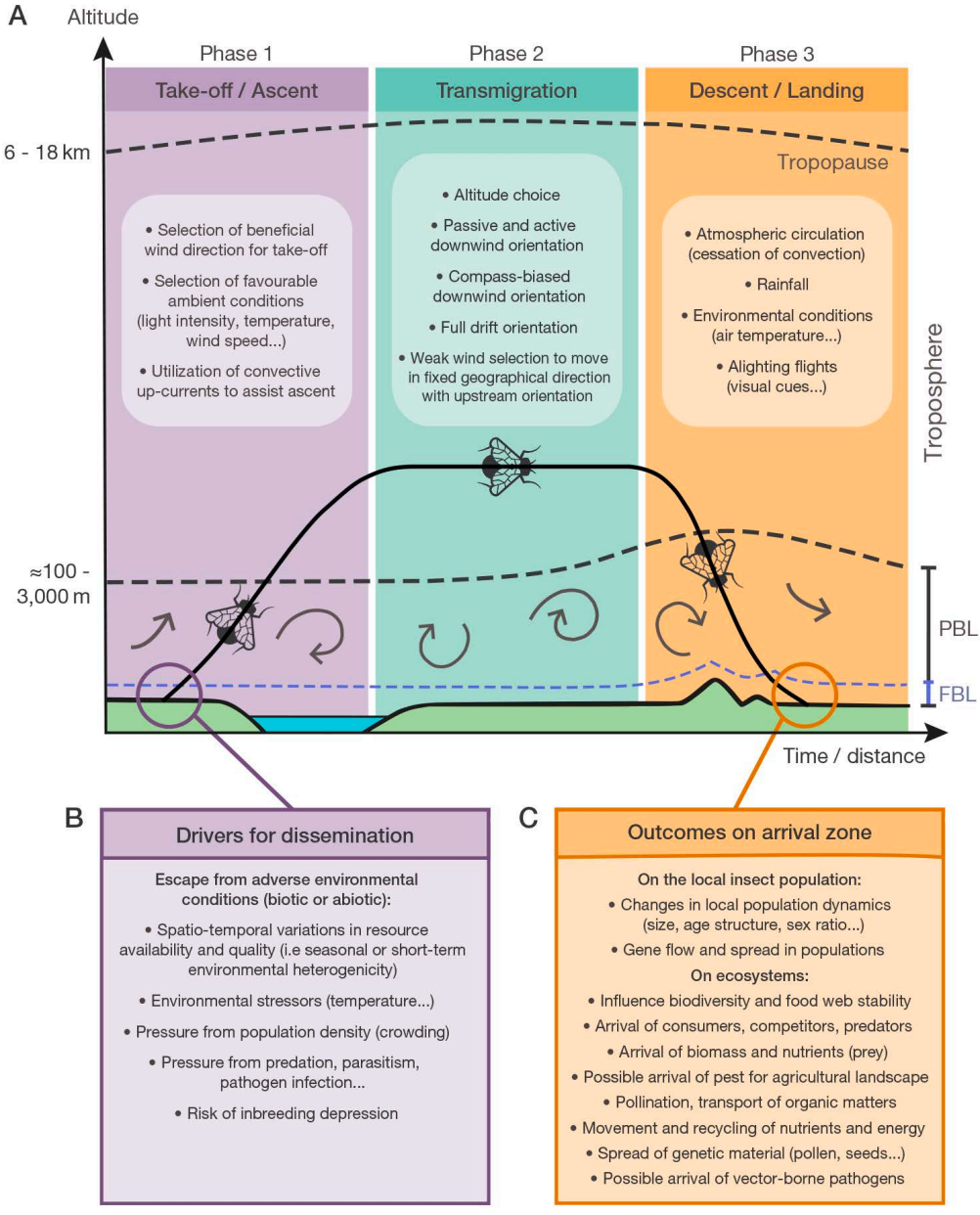

Figure 9.1. Long-distance windborne dissemination of insects: mechanisms and insect control (**A**), drivers (**B**) and outcomes (**C**).

PBL, Planetary Boundary Layer; FBL, Flight Boundary Layer.

Table 9.1. Diversity and biological traits of insect taxa for which there is evidence of high-altitude windborne dissemination.

Order	Family	Species/genera
Coleoptera	Carabidae	carabid beetles sp.; *Zolotarevskyella rhytidera*
	Chrysomelidae	*Ceratoma trifurcata; Chaetocnema coletta; C. pulicaria; Colaspis brunnea; Diabrotica undecimpunctata; D. virgifera; Phyllotreta* sp.
	Coccinellidae	*Coccinella septempunctata; Harmonia axyridis; Hippodamia convergens; H. undecimnotata*
	Curculionidae	*Anthonomus grandis*; *Sitona* sp.
	Dytiscidae	*Hydrovatus* sp.
	Hydrophilidae	*Berosus* sp.
	Staphylinidae	*Paederus fuscipes; P. sabaeus*
Diptera	Ceratopogonidae	*Culicoides flavipunctatus; C. imicola; C. nudipalpis; C. orientalis; C. palpifer; C. brevitarsis*
	Chironomidae	*Chironomus* sp.
	Culicidae	*Aedes vexans; A. argenteopunctatus; A. fowleri; A. quasiunvittatus; A. sollicitans; A. squamiger; A. taeniorhynchus; A. mcintoshi; A vigilax; A. circumluteolus; A. hirsutus; A. vittatus; Anopheles coluzzii; An. gambiae; An. arabiensis; An. coustani; An. pharoensis; An. pulcherrimus; An. rufipes; An. namibiensis; An. squamosus; An. vagus; Culex antennatus; C. watti; C. gelidus; C. perexiguus; C. mali; C. pipiens; C. tarsalis; C. tritaeniorhynchus; C. annulirostris; C. nebulosus; C. bitaeniorhynchus; C. duttoni; C. poicilipes; C. annulioris; Visnui complex; Mansonia uniformis; Lutzi tigripes; Mimomyia mimomyiaformis*
	Drosophilidae	*Drosophilia melanogaster*
	Muscidae	*Stomoxys calcitrans*
	Psychodidae	*Phlebotomus* sp.; *Lutzomyia* spp.
	Simuliidae	*Simulium damnosum*
	Syrphidae	*Episyrphus balteatus, E. corollae*
	Tephritidae	*Bactrocera dorsalis*
Hemiptera	Aleyrodidae	*Bemisia tabaci; Trialeurodes abutilonea; T. vaporariorum*
	Aphididae	*Acyrthosiphon pisum; Aphis craccivora; A. fabae; Lipaphis erysimi; Myzus persicae; Rhopalosiphum maidis; R. padi; Schizaphis graminum; Sitobion avenae; S. miscanthi; Melanaphis sacchari; Toxoptera citricida*
	Berytidae	*Metacanthus nitidus*
	Cicadellidae	*Agallia constricta; Cicadulina mbila; Empoasca fabae; Graminella nigrifons; Macrosteles fascifrons; Neoaliturus tenellus; Nephotettix cincticeps; N. modelatus; N. nigropictus; N. virescens; Recilia dorsalis*

Size / weight*	Ecological trait**	Dissemination capacity (supposed or proven)	References
M	beneficial	36-360 km (*Z. rhytidera*)	Florio *et al.*, 2020; Hu *et al.*, 2016
M	pest, vector	36-360 km (*C. coletta*)	Florio *et al.*, 2020; Kim and Sappington, 2013; Reynolds *et al.*, 2006
M	beneficial	NA	Hodek *et al.*, 1993; Jeffries *et al.*, 2013; Ricci *et al.*, 2005; Roy and Brown, 2015; Siljamo *et al.*, 2020
M	pest, vector	up to >272 km, pot. up to >640–740 km (*A. grandis*)	Kim and Sappington, 2006, 2013; Koralewski *et al.*, 2021
NA	NA	NA	Florio *et al.*, 2020
M	NA	NA	Florio *et al.*, 2020
S, M	beneficial, detrimental	36-360 km	Florio *et al.*, 2020
S	vector	>500 km (*C. imicola*); possibly 500-1000 km (*C. nudipalpis, C. orientalis, C. palpifer, C. flavipunctus*)	Eagles *et al.*, 2014; Jacquet *et al.*, 2016; Lounibos, 2002; Reynolds *et al.*, 2006
S	vector	NA	Reynolds *et al.*, 2006
S	vector	<106 km (*A. taeniorhynchus*); >96.5 km (*A. vigilax*); >177 km (*A. sollicitans*); >61 km (*A. squamiger*); >32 km, even 740 km (*A. vexans*); >25 km (*An. pulcherimus*); >35-200 km (*C. tritaeniorhynchus*); 36-360 km (*A. coluzzi*)	Reynolds *et al.*, 2006; Service, 1997; Yaro *et al.*, 2022
S	model sp	>12 km	Leitch *et al.*, 2021
S	vector	NA	Reynolds *et al.*, 2006
S	vector	NA	Reynolds *et al.*, 2006
S	vector	>500 km	Lounibos, 2002; Reynolds *et al.*, 2006; Satterfield *et al.*, 2020
M	beneficial	>100-200 km	Wotton *et al.*, 2019
M	pest	at least up to 175 km, possibly up to 850 km	Otuka *et al.*, 2019
S	pest, vector	up to 7-10 km (*B. tabaci*)	Byrne, 1999; Crossley and Snyder, 2020; Reynolds *et al.*, 2006
S	pest, vector	1,000-1,500 km (*L. erysimi*); 400 km (*R. maidis*); >160 km (*S. avenae, R. padi, M. persicae*)	Berry and Taylor, 1968; Byrne, 1999; Ghosh *et al.*, 2019; Irwin *et al.*, 1988; Isard *et al.*, 1990; Loxdale *et al.*, 1993; Satterfield *et al.*, 2020; Wang *et al.*, 2019
NA	NA	36-360 km	Florio *et al.*, 2020
S	pest, vector	36-360 km (*N. virescens*)	Florio *et al.*, 2020; Isard *et al.*, 1990; Reynolds *et al.*, 2006

Table 9.1. (continued)

Order	Family	Species/genera
Hemiptera	Delphacidae	*Nilaparvata lugens; Delphacodes kuscheli; Javesella pellucida; Laodelphax striatellus; Perkinsiella saccharicida; Sogatella furcifera; S. kolophon; S. vibix; Tagosodes cubanus; T. orizicolus; Toya propinqua*
	Piesmatidae	*Piesma quadratum*
	Pseudoccocidae	Pse*udococcus njalensis*
	Psyllidae	*Aphalara* sp.; *Cacopsylla affinis; C. melanoneura; C. pruni*
	Pyrrhocoridae	*Dysdercus* sp.
	Reduviidae	*Triatoma infestans*
	Tingidae	*Cysteochila endeca*
	Triozidae	*Trioza urticae*
Hymenoptera	Braconidae	*Microchelonus* sp.
	Megastigmidae	*Megastigmus schimitscheki*
	Scelionidae	*Scelio fulgidus*
Lepidoptera	Crambidae	*Botyodes diniasalis; Conogethes punctiferalis; Cnaphalocrocis medinalis; Ostrinia nubilalis; Spoladea recurvalis*
	Noctuidae	*Agrotis ipsilon; A. infusa; Athetis lepigone; Autographa gamma; Helicoverpa zea; H. armigera Hübner; Heliothis* spp.*; Leucania loreyi; Mythimna convecta; M. separata; Noctua pronuba; Spodoptera exempta; S. exigua; S. frugiperda; Ostrinia nubilalis*
	Nymphalidae	*Danaus plexippus; Vanessa cardui; V. atalanta*
	Plutellidae	*Plutella xylostella*
	Saturniidae	*Hylesia metabus*
	Sphingidae	*Deilephila elpenor; Agrius convolvuli; Hyloicus pinastri; Laothoe populi; Sphinx ligustri*
	Tortricidae	*Choristoneura fumiferana*
Neuroptera	Chrysopidae	*Chrysoperla carnea*
Odonata	Libellulidae	*Pantala flavescens*
	Aeshnidae	*Anax junius*
Orthoptera	Acrididae	*Aiolopus simulatrix; Chortoicetes terminifera; Locusta migratoria; Schistocerca gregaria; Oedaleus senegalensis*
Thysanoptera	Thripidae	*Frankliniella* sp.*; Thrips tabaci*

Size / weight*	Ecological trait**	Dissemination capacity (supposed or proven)	References
S	pest, vector	up to 240 km (*N lugens*)	Hu *et al.*, 2017; Reynolds *et al.*, 2006, 2017
S	vector	NA	Reynolds *et al.*, 2006
S	pest, vector	NA	Reynolds *et al.*, 2006
S	vector	>13 km (*C. melanoneura, C. affinis*); ~50 km (*C. pruni*)	Greenslade *et al.*, 2021
S, M	pest	36-360 km	Florio *et al.*, 2020
L	vector	NA	Lounibos, 2002; Reynolds *et al.*, 2006
NA	NA	NA	Florio *et al.*, 2020
S	vector	>13 km	Greenslade *et al.*, 2021
S	beneficial	36-360 km	Florio *et al.*, 2020
S	pest	NA	Lander *et al.*, 2014
NA	beneficial	NA	Chapman *et al.*, 2015
S, M	pest	NA	Huang *et al.*, 2024; Kim and Sappington, 2013; Reynolds *et al.*, 2016; Sappington, 2018
M, L	pest	>1,000 km (*S. exampta*); up to 1000 km (*A. infusa*); >1,900 km (*A. ipsilon*)	Chapman *et al.*, 2010, 2015; Reynolds *et al.*, 2016; Hu *et al.*, 2016; Sappington, 2018; Wu *et al.*, 2018; Satterfield *et al.*, 2020; Garcia *et al.*, 2021; Farrow and Duly, 1987; Huang *et al.*, 2024
M, L	beneficial	3,600 km (*D. plexippus*,); up to 15,000 km (*V. cardui*)	Mikkola, 2003; Reppert and De Roode, 2018; Stefanescu *et al.*, 2013; Talavera and Vila, 2017
S	pest	NA	Reynolds *et al.*, 2017
M	detrimental	up to 14 km	Ciminera *et al.*, 2019; Jourdain *et al.*, 2012
M, L	pest	NA	Chapman *et al.*, 2010
L	pest	up to 450 km	Reynolds *et al.*, 2016, 2017; Gandiaga and James, 2023
M	pest	NA	Hu *et al.*, 2016; Satterfield *et al.*, 2020
L	patrimonial	17,000 km	Anderson, 2009
L	patrimonial	>600–700 km	Chapman *et al.*, 2015
L	pest	up to 5,000 km (*S. gregaria*); up to 400 km (*C. terminifera*); 300-400 km (*O. senegalensis*)	Chapman *et al.*, 2015; Kutsch *et al.*, 2002; Rennie, 2014; Satterfield *et al.*, 2020
S	vector	NA	Reynolds *et al.*, 2006

*Size/weight: S (<10 mg), M (10 to 70 mg) and L (>70 mg) according to most radar studies (Hu *et al.*, 2016; Huang *et al.*, 2024); when non available, the weight was approximated from the size of the insect. **Significance category: beneficial = pollinator, biocontrol agent, etc.; detrimental = other detrimental effects than pest or vector (e.g., health impacts); patrimonial = charismatic species. NA: lack of information in the literature.

These long-distance disseminations are facilitated by large-scale wind systems such as monsoons, the Gulf Stream, and the Inter-Tropical Convergence Zone (ITCZ), that insects use to conserve energy during long-distance flight, forming cohesive swarms triggered by environmental cues (e.g., many locusts) or dispersing in non-cohesive swarms (Akhter *et al.*, 2023; Reynolds *et al.*, 2017). For example, certain species of black flies, such as *Simulium damnosum,* migrate using the ITCZ that brings them to favorable areas where rain is likely to carry them towards rivers, their larval habitat (Lounibos, 2002). Similarly, in eastern Asia, many lepidopteran and planthopper species use the monsoon system each year to facilitate their northward migration in spring and southward return at the end of summer, along an aerial corridor named the East Asian Insect Flyway (EAIF; Hu *et al.*, 2025).

Moreover, severe and rare weather events like hurricanes and cyclones can also transport insects over great distances quickly, often leading to the colonization of new regions (Gillespie *et al.*, 2012; Reynolds *et al.*, 2017; Zimmerman, 1948). These storms usually follow predictable tracks, dispersing wind-borne organisms in consistent directions. For instance, in the northeast Pacific, hurricanes travel from east to west (Gillespie *et al.*, 2012). There are many documented examples of this type of long-distance insect movement caused by these extreme phenomena, like the fast expansion of the boll weevil *A. grandis* in the US, or that of the African locust *S. gregaria* in the Windward Islands (Caribbean) through either a hurricane or the peculiar dynamics of the Azores-Bermuda ridge and strong trade winds (Culin *et al.*, 1990; Kim and Sappington, 2013; Richardson and Nemeth, 1991).

In light of the above observations, insect migration can be categorized into different spatio-temporal patterns (Gao *et al.*, 2020; Johnson, 1969; Satterfield *et al.*, 2020; Service, 1997): (i) the classic round-trip migration, observed mainly in certain butterflies, dragonflies, ladybirds, noctuid moths and hoverflies. One of the most studied examples is the monarch butterfly *D. plexippus*, which presents a round trip migration between Canada and Mexico taking up to five generations to complete (Reppert and De Roode, 2018); (ii) a more complex interconnected network of migration across continents, illustrated by the migration of the desert locust *S. gregaria,* from Africa to Asia, and even from Africa to the Caribbean; and (iii) seasonal migration simply radiating out from the source sites, characteristic of small insects such as aphids.

How insects control their dissemination

Contrary to other particles disseminating in the atmosphere (bacteria, spores of fungi, seeds), insect windborne dissemination is not entirely passive; rather, it involves a range of quasi-passive and active flight behaviours. These behaviours allow insects to exert some control over their movement, which remains predominantly influenced by wind patterns. This control can be present during either one or multiple phases of migration (Figure 9.1A): emigration (take-off/ascend), transmigration, or immigration (descent/landing) (Chapman *et al.*, 2015; Gao *et al.*, 2020; Reynolds *et al.*, 2016). Overall, migration strategies among insects seem to vary greatly depending on their size and intrinsic flight capabilities (Reynolds *et al.*, 2016).

Even small weak-flying insects can influence their migratory patterns by choosing specific times for take-off and landing, and making altitude adjustments, thus

exhibiting quasi-passive flight (Gao *et al.*, 2020; Reynolds *et al.*, 2016, 2017). For example, the potato leafhopper *Empoasca fabae* shows greater migration in autumn conditions favorable to southward transport toward its overwintering shelter sites (Gao *et al.*, 2020). Additionally, recent radar studies of nocturnal insects in East China revealed that spring migrants showed evidence of wind selectivity, choosing to fly on nights with the most favorable winds (i.e. winds going northward) (Huang *et al.*, 2024). But most weak fliers, like most hemipterans, whose dissemination paths closely match prevailing wind directions, do not seem to select beneficial winds (Hu *et al.*, 2016). Instead, the timing of take-off and landing is often influenced by ambient conditions such as light intensity and temperature. Moreover, a consistent circadian pattern in migratory insect movement can be observed, with migratory activity peaking around dawn, noon or dusk, depending mainly on the taxa involved (Haest *et al.*, 2024). For example, mass take-offs of certain insects are known to occur at dusk or dawn (common examples include planthoppers and leafhoppers), stimulated by light intensity, when conditions are optimal for their migration (Johnson, 1969; Reynolds *et al.*, 2006, 2017). Conversely, for day-migrants, including most small weak-flying insects such as aphids or some mosquitoes, the take-off and ascent tend to happen over a more extended period during the day, utilizing convective updrafts caused by the surface warming by the sun to assist their ascent (Reynolds *et al.*, 2006). For these taxa, the initiation of flight is usually manifested by a sustained upward flight taking the insect out of its FBL, where it can be carried by the wind, as observed in multiple mosquitoes of the *Aedes* species and in aphids (Reynolds *et al.*, 2006; Service, 1997). Initiation of flight also seems to require temperatures greater than, and wind speed less than, certain thresholds, as corroborated by many radar observations (Chapman *et al.*, 2015; Isard *et al.*, 1990; Johnson, 1969; Reynolds *et al.*, 2017). But temperature does not only act as a threshold, sometimes it can also act as a cue for take-off, as reported for the green darner dragonfly, *Anax junius*, where flight initiation seems to be triggered by decreasing autumn temperatures (Chapman *et al.*, 2015; Wikelski *et al.*, 2006).

Concerning the termination of flight, it can be guided by visual cues and environmental conditions. For example, some nocturnal migrations are clearly terminated by air temperatures falling below the threshold required for the insect to keep flying, especially in temperate regions (Reynolds *et al.*, 2006). Meanwhile, atmospheric circulation alone can bring some weak-flying diurnal species back to the ground, most of them descending as convection diminishes before nightfall (Berry and Taylor, 1968; Reynolds *et al.*, 2017). Rainfall is another significant factor disrupting steady long-distance insect migration, with radar evidence indicating the end of migration under heavy rain (Reynolds *et al.*, 2017). Thus, most insects do not seem to have much information about the suitability of their landing site before they start descending closer to the ground. However, some may undertake "alighting flights" toward suitable landing sites, as observed in many whiteflies and aphids. In particular, studies on the black bean aphid, *Aphis fabae,* suggest that insects seem to respond to "vegetative" cues such as the wavelength of light reflected from plants, or odors (Reynolds *et al.*, 2006). Unlike ascent, descent remains the least understood phase of migration. There is no synchronous mass descent of insects at the end of migration, and individuals seem to fall out of the air mass over a more extended period (Reynolds *et al.*, 2006).

In addition to selecting the timing of take-off and landing, medium to large insects can exhibit more pronounced active orientation behaviours than smaller ones, optimizing their paths through complex interactions with the wind and other environmental cues (Gao *et al.*, 2020; Hu *et al.*, 2016; Reynolds *et al.*, 2016, 2017). Medium-sized insects generally orient themselves and actively fly in or close to the downwind direction, maximizing their travel distance. It is hypothesized that this strategy is adaptive in nature and thus is particularly found in regions where seasonally prevailing winds lead to suitable habitats (e.g., seasonal ITCZ in West Africa), or where favorable destination zones can be located in any direction from the source area. Overall, this is the most common wind-related strategy observed in medium-sized, high-flying insects (Chapman *et al.*, 2010; Hu *et al.*, 2016; Reynolds *et al.*, 2016). For example, in the Sahel, monsoonal and harmattan winds take the migrants (mainly Coleoptera) in seasonally appropriate directions, making wind selection or trajectory correction useless (Florio *et al.*, 2020). Some larger insects (i.e., stronger flyers), such as the silver Y moth, *A. gamma*, can also demonstrate compass-biased downwind orientation (CBDO). This strategy involves migrating in a seasonally preferred direction, with some degree of compensation for cross-wind drift (i.e., trajectory correction) when necessary. In this species, migration is usually initiated on days or nights when winds are favorable, and suppressed when they are not, and insects often choose altitudes with the fastest wind to optimize their movement (Chapman *et al.*, 2010, 2015; Reynolds *et al.*, 2016, 2017). However, studies of this mechanism for a wider taxonomic and geographical range are lacking. Theoretically, this behavior would significantly enhance migration success by allowing insects to efficiently cover large distances. In some rare cases, insects can exhibit (almost) full drift, where their orientation remains approximately constant regardless of wind direction. This strategy may be beneficial for ensuring seasonal movements despite varying wind conditions but remains extremely rare and is only observed in larger, strong fliers (Reynolds *et al.*, 2016). Alternatively, certain large insects can detect weak high-altitude winds that allow them to move in a fixed geographical direction with an upwind component –without needing to compensate for drift– thus maintaining a constant compass direction with upwind displacement (Reynolds *et al.*, 2016). Overall, extensive radar data have demonstrated that in medium- and large-size insects, wind-related orientations and adaptive wind selectivity are highly common mechanisms, suggesting that compass-based navigation is likely a universal trait in medium and large insect migrants (Hu *et al.*, 2016; Reynolds *et al.*, 2017).

Orientation behaviours during high-altitude migration, as well as the timing of flight, are influenced by various environmental cues, such as local topography, celestial cues, the position of the sun, the Earth's magnetic field, temperature gradients, wind patterns, and photoperiods (Akhter *et al.*, 2023; Reynolds *et al.*, 2016). To detect these cues and maintain their orientation during flights, insects rely on various and sophisticated sensory modalities. Visual perception of ground pattern and movement, which is often used by low altitude insect migrants, is less effective at high altitude due to reduced visibility. Instead, insects may rely on cues from the wind itself. For example, some can detect fluctuations in turbulent velocity and/or turbulent "jerks" (i.e., rapid changes in acceleration), which help them determine the mean wind direction and maintain a downwind orientation (Reynolds *et al.*, 2016).

⏩ Windborne dissemination: Traits and consequences at the insect scale

The biology of disseminating insects

Over time, insects have evolved a range of biological traits facilitating dissemination (Renault, 2020). These traits often include specialized structures such as wings of various forms and modified legs that enhance their ability to move and colonize new environments, as well as various modifications in muscle morphology, neuroendocrine regulation and energy metabolism (Asplen, 2018; Renault, 2020; Warfvinge *et al.*, 2017). For windborne dissemination of winged insects, wing morphology is a key factor influencing dissemination capabilities. For instance, in the migratory monarch, *D. plexippus*, longer and larger wings are associated with better flight performance and longer dissemination distances (Renault, 2020). Similarly, itinerant Trichoptera species from the genus *Ecnomus* show greater wing size and shape than resident species of the same genus (Lancaster and Downes, 2017). But wings are not the only important trait for windborne dissemination. Insect resistance to atmospheric conditions in the air masses (UV radiation, cold, desiccation, etc.) may also be a key factor in their dissemination capacity. Unfortunately, the references concerning these aspects are rare for insects, unlike other organisms such as bacteria (see Chapter 5). But the numerous studies on insect cold resistance suggest that they could have a great capacity to endure extreme conditions at high altitudes for a long time (Bale, 2002). Moreover, dissemination polymorphism, where different individuals within a species exhibit distinct dispersal capabilities, is also common in multiple insect groups, including Coleoptera, Heteroptera, Hemiptera, or Orthoptera. This polymorphism often manifests itself as variations in wing morphology, with alate (winged) or macropterous (long-winged) dispersers, and apterous (non-winged) or brachypterous (short-winged) residents/sedentary individuals. Notable examples include the planthopper, *N. lugens*, crickets like *Gryllus lineaticeps* and various aphid species (Renault, 2020; Sun *et al.*, 2020; Zera and Denno, 1997). Additionally, dispersal polymorphism can influence other traits such as body size, metabolic rate, and specific behaviours that enhance dispersal success. For instance, larger body size and lower metabolic rate can enhance the dispersal abilities of certain individuals within a species (Cote *et al.*, 2017; Renault, 2020).

But these adaptations to dispersal incur several costs and trade-offs, particularly in wing dimorphic insects where pre-departure costs (i.e., the development and maintenance of wings and flight muscles) can be substantial. These costs often result in reduced reproductive/ovarian investment or success for dispersing individuals, especially since dispersal often occurs before the start of reproduction in these species. This phenomenon is often referred to as the "oogenesis-flight syndrome" (Lorenz, 2007; Renault, 2020; Zera and Denno, 1997). This trade-off between reproduction and dispersal is evident in wing-dimorphic insects like the bog myrtle aphid *Myzocallis myricae* where macropterous (dispersing) individuals tend to have lower reproductive rates compared to their brachypterous (non-dispersing) counterparts (Dixon and Kindlmann, 1999), or the cricket *Gryllus bimaculatus,* where there is a clear trade-off between egg production and flight capability (Lorenz, 2007). Nevertheless, the reproductive cost of migration is also evident in monomorphic species. For example, a

recent study on the Nymphalini butterflies tribe showed that non-migratory species (i.e., *Aglais urticae*, *A. io* and *Polygonia c-album*) had higher lifetime fecundity and higher reproductive investment than migratory species (i.e., *V. cardui* and *V. atalanta*) (Wiklund and Friberg, 2022). Moreover, the cost of the energy consumed during the flight itself adds to the costs of migration and can also have transgenerational fitness costs. In the black-and-red-bug *Lygaeus equestris* (Heteroptera) for example, winged individuals produce smaller eggs, which are more sensitive to environmental stresses such as starvation, indicating a trade-off between dispersal and offspring quality (Renault, 2020; Solbreck and Sillén-Tullberg, 1990). Finally, the act of migration itself also presents risks, including transport to unsuitable habitats and possible exposure to predators, increasing the potential cost of migration yet again. For example, in lepidopterans, which typically engage in substantial premigratory lipid accumulation as well as feeding "en route" to sustain the energy requirements of their flight, a higher body mass may increase susceptibility to avian predators (via reduced acceleration capacity and slower rotational capacity and evasive maneuvers) (Renault, 2020; Srygley and Dudley, 2007). Moreover, a disparity in investment in migration can sometimes be observed between sexes. For example, in the South African grasshopper *Phymateus morbillosus*, females are too heavy to lift themselves for active flight, probably because of an investment in reproduction rather than in dissemination, while the males can show active flight patterns for short periods of time (Kutsch *et al.*, 2002).

Consequences on insect biology, ecology and evolution

Despite their costs, long-distance movements have many benefits for insects. Escape from adverse environmental conditions is a primary driver, with migration and dispersal being adaptive strategies evolved mainly in response to environmental heterogenicity (Figure 9.1B; Asplen, 2018; Reynolds *et al.*, 2017; Talavera and Vila, 2017).

The specific behavioral process of migration, primarily driven by the spatiotemporal variations in resource availability, can result in a significant spatial redistribution of insect populations when followed by reproduction. Hence, this migration syndrome has evolved as a response to seasonal or shorter-term changes in resource quality and availability (Reynolds *et al.*, 2017; Talavera and Vila, 2017). Thus, it enables insects to optimally exploit temporary resources, whether local or distant, thereby playing a vital role in their survival, reproduction, and evolutionary success (Talavera and Vila, 2017). This phenomenon is evident in the evolution of adaptive traits such as wing polymorphism and other above mentioned traits (Mazzi and Dorn, 2012).

More generally, migration is driven by evasion of detrimental conditions such as harmful abiotic and/or biotic factors (e.g., temperature). For example, many jumping plant lice (Hemiptera) migrate to overwintering sites each year to evade harmful temperatures (Greenslade *et al.*, 2021; Hodkinson, 2009). Moreover, migration is also often triggered by low food quality and/or quantity. For example, in ladybirds such as *Coccinella septempunctata* and *Harmonia axyridis*, low abundance of their aphid prey seems to be an important cue for long-distance dispersal (Jeffries *et al.*, 2013). Many other biotic factors can also influence the extent and nature of these migratory behaviours. Among others, population density, as well as the presence of natural enemies (predation, parasitism) are key components. For example, the degree of crowding experienced during development, as well as host quality, will largely determine

whether or not insects like aphids or the western cherry fruit fly, *Rhagoletis indifferens*, will produce winged individuals and disperse or not (Dixon and Kindlmann, 1999; Mazzi and Dorn, 2012). This can also be observed in some mosquitoes (e.g., *Aedes taeniorhynchus*) where high larval density seems to produce a migrant phase in adults (Service, 1997). Similarly, in the butterfly *V. cardui*, significant modifications in gene expression, particularly within hormonal pathways hypothesized to play a role in regulating the timing of migration in females, as well as development, reproduction and metabolism, were observed in response to host plant availability and larval crowding (Shipilina *et al.*, 2024). Meanwhile, in the pea aphid, *Acyrthosiphon pisum*, the proportion of winged offspring increases with population exposure to natural enemies (Sloggett and Weisser, 2002; Weisser *et al.*, 1999).

Hence, migration shows multiple adaptive benefits for insect populations. First, it affects survival and allows the colonization of new habitats or hosts. For example, while many insects enter diapause or quiescence to survive unfavorable periods, migratory species can theoretically breed continuously and exploit a succession of favorable breeding grounds, thus achieving more generations per year than non-migrating species, as in the genus *Heliothis* (Farrow and Duly, 1987; Reynolds *et al.*, 2017). However, this is highly taxon-dependent. Moreover, it also offers temporary enemy-free space, reducing predation, parasitism, and pathogen infection (Altizer *et al.*, 2011; Chapman *et al.*, 2015). Additionally, migration affects gene flow as well, allowing the avoidance of inbreeding depression at the natal site, even more so for species where one sex disperses more than the other. Finally, it also influences population dynamics by altering the age structure, sex ratio, and mating status of the population, as well as the spread of adaptive genes, such as those for insecticide resistance. Thus, it is a major life-history variable for any species that migrates over long distances (Asplen, 2018; Farrow and Duly, 1987; Kim and Sappington, 2013).

⏩ Ecological impacts of insect dissemination at the ecosystem scale

Quantitative studies highlight the massive scale of insect migration. For example, it is estimated that 3.5 trillion insects, weighing 3,200 tons in total, migrate annually above the southern part of the United Kingdom (Hu *et al.*, 2016). Meanwhile, that number reaches 9.3 trillion nocturnal insect migrants, weighing 15,000 tons in total, above East China, one of the biggest food production regions in China and one of the most densely populated agricultural areas in the world (Huang *et al.*, 2024). Considering the scale and magnitude of this phenomenon, it is crucial to understand the impact of the dissemination of insects in the atmosphere on ecosystems (Figure 9.1C).

The ecological impacts of insect migrants are multifaceted, involving both direct and indirect effects, possibly beneficial or detrimental, influencing ecosystem services, processes and biogeochemistry (Chapman *et al.*, 2015; Reynolds *et al.*, 2006; Satterfield *et al.*, 2020).

Direct "trophic" effects occur when there is a mass arrival of consumers, competitors, predators or prey, which structure food webs and biodiversity patterns in ecosystems (Bauer and Hoye, 2014; Reynolds *et al.*, 2017; Satterfield *et al.*, 2020). Some effects are beneficial, such as the biological control of pests. For example, the marmalade hoverfly

Episyrphus balteatus larvae feed on aphid pests after its migration across the Mediterranean Sea into Europe (Wotton *et al.*, 2019). Migratory insects also provide significant food resources for higher trophic levels, including many birds and mammals. Thus, the periodic arrival of migratory insects can provide vital food resources for their predators, supporting their populations during critical periods (Bauer and Hoye, 2014; Chapman *et al.*, 2015; Reynolds *et al.*, 2017; Satterfield *et al.*, 2020). For instance, aerial insectivores and grizzly bears feed on migrating army cutworms *Euxoa auxiliaris* (Bauer and Hoye, 2014), while migrating birds like the Amur falcon probably feed largely on migrating dragonflies (*Pantala flavescens*) during migration, as both species share similar migratory routes (Anderson, 2009; Chapman *et al.*, 2015). However, other effects are detrimental. Indeed, this influx of insects can lead to competition with resident species for shared resources or altering interactions through shared predators, which may have cascading effects on predator-prey dynamics, influencing biodiversity and ecosystem stability (Chapman *et al.*, 2015; Reynolds *et al.*, 2017; Satterfield *et al.*, 2020). This is especially true for invasive species, like for example the sweet potato whitefly *Bemisia tabaci* (Crossley and Snyder, 2020; Pretorius *et al.*, 2023). Chapter 12 presents further information about the consequences of invasion by airborne organisms on ecosystems. Many migrating insect species are also well-known pests for agricultural landscape, such as the desert locust *S. gregaria*, aphids or moths, and can cause substantial economic damage to crops. Their long-range movement further increases their pest status by making management more difficult (Bauer and Hoye, 2014; Farrow and Duly, 1987; Mazzi and Dorn, 2012; Pedgley, 1993; Reynolds *et al.*, 2006).

In contrast, indirect "transport" effects involve many beneficial effects such as the delivery of ecosystem services including pollination, the transport of organic matter, or the movement and recycling of nutrients and energy (through feeding, excretion, reproduction and decomposition). These can enhance soil fertility and plant growth and are critical for overall ecosystem health (Bauer and Hoye, 2014; Chapman *et al.*, 2015; Reynolds *et al.*, 2017; Satterfield *et al.*, 2020). The hoverfly *E. balteatus* is once again a good example as the adults pollinate a large diversity of plants during their migration across de the Mediterranean Sea, while in eastern Asia, it was estimated that it could visit at least 1012 flowering plant species belonging to 39 orders during their windborne migration, making them great pollinators in addition to the other ecosystem services they provide (Jia *et al.*, 2022; Wotton *et al.*, 2019). Insects also act as "genetic links" facilitating the spread of genetic material, either through the migrants themselves (allowing, for example, the maintenance of genetic susceptibility to insecticides by diluting resistant genes), or by carrying pollen, seeds, and other propagules (Bauer and Hoye, 2014; Reynolds *et al.*, 2017; Satterfield *et al.*, 2020). These roles highlight the importance of insects in connecting distant ecosystems and maintaining ecological balance. Nevertheless, the transport of all these particles and genetic materials by insects can also cause harmful effects, particularly when insects act as vectors for parasites or pathogens affecting plants, animals, and humans (Crossley and Snyder, 2020; Ghosh *et al.*, 2019; Huestis *et al.*, 2019; Lefèvre *et al.*, 2022), or when they spread genes such as those for insecticide resistance (Bauer and Hoye, 2014; Chapman *et al.*, 2015; Kim and Sappington, 2013; Reynolds *et al.*, 2017). For instance, arboviruses such as dengue, West Nile virus or Chikungunya are becoming global threats to human health, spreading from sub-Saharan Africa to most areas of the world due to the dissemination of their mosquito vectors (Rezza, 2014).

⏩ Conclusions

The study of high-altitude insect dissemination in the air masses has rapidly advanced due to new methodological developments and technologies, allowing surprising aspects of insect migration and dispersal behaviours to be revealed and improving our understanding of these phenomena. Mainly, studies of this phenomenon have revealed how extensively insects of various taxa utilize atmospheric currents and have challenged assumptions about their migratory limits and control over their dissemination. They have also highlighted that many species, even those previously thought to migrate only within their FBL, also engage in long-distance windborne transport at high altitudes. For example, *D. plexippus* and *V. cardui* butterflies have been observed migrating at altitudes up to 1 km under favorable wind conditions, utilizing both within-FBL and above-FBL migratory flight, even if they were previously thought to migrate only within the FBL (Chapman *et al.*, 2010, 2015; Reppert and De Roode, 2018; Stefanescu *et al.*, 2013). This quasi-passive form of transport relies on meteorological conditions and has evolved as a highly effective mechanism for dissemination, allowing insects to travel vast distances that would be inaccessible through active flight alone, often crossing geographical and ecological barriers, enhancing their fitness and colonization capabilities (Reynolds *et al.*, 2006, 2017). Yet, while high-altitude insect migration may appear to be mostly influenced by wind currents, recent studies reveal a more nuanced picture, showing that insects can actively adjust their flight orientations, take-off and landing times, and utilize environmental cues to optimize their migration strategies (Chapman *et al.*, 2015; Gao *et al.*, 2020; Reynolds *et al.*, 2016). Insect windborne dissemination is thus far less passive than previously thought. These approaches and technologies are discussed in more detail in Chapter 11.

Dissemination plays a pivotal role in shaping insect ecological and evolutionary dynamics across ecosystems. The "migratory" traits (i.e., characteristics associated with migration that insects have developed to facilitate long-distance movement), such as specialized structures, dispersal polymorphism, and trade-offs with reproductive investment, highlight the complex interplay between dissemination capabilities and other fitness traits (Asplen, 2018; Lorenz, 2007; Renault, 2020). These traits provide significant advantages for escaping unfavorable conditions and accessing ephemeral resources, which are essential for survival in spatially and temporally heterogeneous environments (Reynolds *et al.*, 2017; Talavera and Vila, 2017). However, the ecological consequences of insect dissemination extend far beyond individual fitness: they impact population dynamics, gene flow, and ecosystems. Indeed, migratory and windborne insects play essential roles in nutrient transport, pollination, pest control, and food web dynamics (e.g., by acting as prey or predators) among others (Bauer and Hoye, 2014; Chapman *et al.*, 2015; Hu *et al.*, 2016; Satterfield *et al.*, 2020). While many of these effects are beneficial, the potential for harmful consequences –particularly related to pathogens/disease spread and competition with local species– underscores the importance of understanding and managing insect movements within the context of ecosystem health, agricultural management, and public health.

However, a noticeable bias in research dealing with insect long-distance windborne dissemination can be observed. Indeed, most of the studies focused on economically or ecologically important taxa with the most overall impact on food and human health, or large, charismatic species (Table 9.1). Consequently, mosquitoes, aphids, or noctuid

moths are well-represented due to their roles as pests and vectors, whereas other taxa, such as Hymenoptera, are underrepresented in current studies despite documented evidence of long-distance dissemination in species such as parasitoid wasps (Hu *et al.*, 2016; Taylor, 1974). Such biases underscore the need for more comprehensive studies, incorporating broader taxonomic and ecological perspectives, to accurately assess the scale and ecological implications of aerial dissemination across insect species.

Analysis of Table 9.1 also suggests that dissemination capacity cannot simply be predicted based on taxonomy or body size/mass alone. For instance, although many mosquitoes disseminate via windborne transport, the Asian tiger mosquito, *Aedes albopictus,* primarily spreads through human-mediated means, such as transportation in car tires, rather than through atmospheric currents (Lounibos, 2002; Rezza, 2014). However, there is a tendency for larger migrating species to have more means of control over their dissemination and therefore more dissemination capacity. Neverthless, many larger insect species still do not disseminate via the atmosphere (e.g., within FBL-migrating butterflies and dragonflies) (Chapman *et al.,* 2010, 2015). This complexity suggests that the dissemination potential of each species is shaped by a combination of intrinsic traits and environmental interactions rather than solely by size or taxonomic classification. Overall, Table 9.1 underscores the massive presence in the atmosphere of a wide range of insect species and the significant role of windborne dissemination in their long-distance movement.

Altogether, insect high-altitude migration presents unique traits compared to the migrations of other taxa. Unlike birds, which typically complete their migrations within a single generation, insects may rely on multiple generations to complete migration cycles due to their short lifespan, as seen in migratory species like *V. cardui* (Chapman *et al.*, 2011, 2015; Satterfield *et al.*, 2020; Stefanescu *et al.*, 2013). Additionally, insect ability to migrate both actively and passively (within and above their FBL) distinguishes them from most vertebrates, which generally migrate actively, and from plants or fungi, which primarily rely on passive dissemination (Osborne *et al.*, 2002). Finally, vertebrates are usually able to forage as well as migrate at high altitude, while as we previously mentioned, insects observed at high altitudes are usually only engaged in migration (Reynolds *et al.*, 2017). Moreover, while this review has focused on insects, some of these dissemination mechanisms can also extend to other small terrestrial arthropods, such as some spiders, which use "ballooning" to disperse, and may travel similarly through atmospheric currents (Suter, 1999; Reynolds *et al.,* 2007). However, these phenomena seem much less studied in other arthropods. Nonetheless, these examples illustrate the wider applicability of these dissemination mechanisms across small organisms, highlighting the interconnectedness of airborne ecological networks.

In conclusion, understanding the adaptative and ecological dimensions of insect dissemination is essential, especially in light of rapid environmental changes. Indeed, the severe decline in insect populations, the potential alterations in their migratory patterns, and the possible increases in their metabolic flight costs due to climate change and human activities underline the need to better understand insect dissemination and its consequences, as these changes can have cascading effects on ecosystems, agriculture, and health, given their multitude of ecological roles (Bebber *et al.*, 2013; Kling and Ackerly, 2020; Parlin *et al.*, 2023; Sánchez-Bayo and Wyckhuys, 2019;

Satterfield *et al.*, 2020). For example, it has been shown that the increase in temperature resulting from climate change intensifies the baseline energy expenditure in the monarch butterfly, *D. plexippus*, for which daily energy expenditure has been gradually increasing since 1961 (Parlin *et al.*, 2023). Moreover, invasive insects alone were estimated to cost a minimum of US $70 billion per year globally, with associated health costs exceeding US $6.9 billion per year (Bradshaw *et al.*, 2016), while being the second most important invasive taxa (after vascular plants) in terms of species numbers, as highlighted in a recent IPBES report (IPBES, 2023). Consequently, the need for better surveillance and prophylaxis strategies to anticipate and mitigate vector-borne disease and pest emergence, as well as bioinvasions, is a growing discussion within the scientific community, particularly from a One Health perspective (Morris *et al.*, 2022; Soubeyrand *et al.*, 2024).

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⏩ Literature cited

Akhter T., *et al.*, 2023. Going places: Insect migration. *Resonance*, 28 (1), 71-84. https://doi.org/10.1007/s12045-023-1527-2

Alerstam T., *et al.*, 2003. Long-distance migration: Evolution and determinants. *Oikos*, 103 (2), 247-260. https://doi.org/10.1034/j.1600-0706.2003.12559.x

Altizer S., *et al.*, 2011. Animal migration and infectious disease risk. *Science*, 331 (6015), 296-302. https://doi.org/10.1126/science.1194694

Anderson R.C., 2009. Do dragonflies migrate across the western Indian Ocean? *Journal of Tropical Ecology*, 25 (4), 347-358. https://doi.org/10.1017/S0266467409006087

Asplen M.K., 2018. Dispersal strategies in terrestrial insects. *Curr. Opin. Insect Sci.*, 2716-20. https://doi.org/10.1016/j.cois.2018.01.009

Bale J.S., 2002. Insects and low temperatures: From molecular biology to distributions and abundance. *Philos. Trans. R. Soc. B Biol. Sci.*, 357 (1423), 849-862. https://doi.org/10.1098/rstb.2002.1074

Bauer S., Hoye B.J., 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344 (6179), 1242552. https://doi.org/10.1126/science.1242552

Bebber D.P., *et al.*, 2013. Crop pests and pathogens move polewards in a warming world. *Nature Climate Change*, 3 (11), 985-988. https://doi.org/10.1038/nclimate1990

Berry R.E., Taylor L.R., 1968. High-altitude migration of aphids in maritime and continental climats. *J. Anim. Ecol.*, 37 (3), 713. https://doi.org/10.2307/3084

Bradshaw C.J.A., *et al.*, 2016. Massive yet grossly underestimated global costs of invasive insects. *Nat. Comm.*, 7 (1), 12986. https://doi.org/10.1038/ncomms12986

Byrne D., 1999. Migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. *Agric. For. Meteorol.*, 97 (4), 309-316. https://doi.org/10.1016/S0168-1923(99)00074-X

Chapman J.W., *et al.*, 2010. Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science*, 327 (5966), 682-685. https://doi.org/10.1126/science.1182990

Chapman J.W., *et al.*, 2011. Recent insights from radar studies of insect flight. *Annu. Rev. Entomol.*, 56, 337-356. https://doi.org/10.1146/annurev-ento-120709-144820

Chapman J.W., *et al.*, 2015. Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters*, 18 (3), 287-302. https://doi.org/10.1111/ele.12407

Ciminera M., *et al.*, 2019. Genetic variation and differentiation of *Hylesia metabus* (Lepidoptera: Saturniidae): Moths of public health importance in French Guiana and in Venezuela. *Journal of Medical Entomology*, 56 (1), 137-148. https://doi.org/10.1093/jme/tjy167

Clobert J., *et al.*, 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12 (3), 197-209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Cote J., *et al.*, 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, 40 (1), 56-73. https://doi.org/10.1111/ecog.02538

Crossley M.S., Snyder W.E., 2020. What is the spatial extent of a *Bemisia tabaci* population? *Insects*, 11 (11), 813. https://doi.org/10.3390/insects11110813

Culin J., *et al.*, 1990. A simulation model examining boll weevil dispersal: Historical and current situations. *Environ. Entomol.*, 19 (2), 195-208. https://doi.org/10.1093/ee/19.2.195

Dingle H., 2014. *Migration: The biology of life on the move*, New York, Oxford University Press, 326 p. https://doi.org/10.1093/acprof:oso/9780199640386.001.0001

Dingle H., Drake V.A., 2007. What is migration? *BioScience*, 57 (2), 113-121. https://doi.org/10.1641/B570206

Dixon A.F.G., Kindlmann P., 1999. Cost of flight apparatus and optimum body size of aphid migrants. *Ecology*, 80 (5), 1678-1690. https://doi.org/10.1890/0012-9658(1999)080[1678:COFAAO]2.0.CO;2

Dung W.S., 1981. General survey on seasonal migrations *Nilaparvata lugens* (Stal) and *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae) by means of airplane collections [in Chinese with English summary]. *Acta Phytophylacica Sinica*, 73-81.

Eagles D., *et al.*, 2014. Long-distance aerial dispersal modelling of *Culicoides* biting midges: Case studies of incursions into Australia. *BMC Vet. Res.*, 10 (1), 135. https://doi.org/10.1186/1746-6148-10-135

Farrow R.A., Duly J.C., 1987. Long-range movements as an adaptive strategy in the genus *Heliothis* (Lepidoptera: Noctuidae): A review of its occurrence and detection in four pest species. *Australian Journal of Zoology*, 35 (1), 1-24. https://doi.org/10.1071/ZO9870001

Florio J., *et al.*, 2020. Massive windborne migration of Sahelian insects: Diversity, seasonality, altitude, and direction. *bioRxiv*, 2020.02.28.960195. https://doi.org/10.1101/2020.02.28.960195

Gandiaga F., James P.M.A., 2023. Quantifying long-distance dispersal of an outbreaking insect species using trap capture data and phenology. *Forest Ecology and Management*, 544, 121187. https://doi.org/10.1016/j.foreco.2023.121187

Gao B., *et al.*, 2020. The 'migratory connectivity' concept, and its applicability to insect migrants. *Movement Ecology*, 8 (1), 48. https://doi.org/10.1186/s40462-020-00235-5

Garcia A.G., *et al.*, 2021. Ecological modelling of insect movement in cropping systems. *Neotropical Entomology*, 50 (3), 321-334. https://doi.org/10.1007/s13744-021-00869-z

Ghosh S., *et al.*, 2019. Effect of regional wind circulation and meteorological factors on long-range migration of mustard aphids over indo-gangetic plain. *Sci. Rep.*, 9 (1), 5626. https://doi.org/10.1038/s41598-019-42151-8

Gillespie R.G., *et al.*, 2012. Long-distance dispersal: A framework for hypothesis testing. *Trends Ecol. Evol.*, 27 (1), 47-56. https://doi.org/10.1016/j.tree.2011.08.009

Greenslade A.F.C., *et al.*, 2021. High-altitude migration of *Psylloidea* (Hemiptera) over England. *Entomologist's Gazette*, 72 (3), 189-198. https://doi.org/10.31184/G00138894.723.1817

Haest B., *et al.*, 2024. Continental-scale patterns in diel flight timing of high-altitude migratory insects. *Philos. Trans. R Soc. Lond. B Biol. Sci.*, 379, 20230116. https://doi.org/10.1098/rstb.2023.0116

Hodek I., *et al.*, 1993. Long-distance flights on *Coccinellidae* (Coleoptera). *Eur. J. Entomol*, 90, 403-414.

Hodkinson I.D., 2009. Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): A global synthesis. *Journal of Natural History*, 43 (1-2), 65-179. https://doi.org/10.1080/00222930802354167

Hu G., *et al.*, 2016. Mass seasonal bioflows of high-flying insect migrants. *Science*, 354 (6319), 1584-1587. https://doi.org/10.1126/science.aah4379

Hu G., *et al.*, 2017. Population dynamics of rice planthoppers, *Nilaparvata lugens* and *Sogatella furcifera* (Hemiptera, Delphacidae) in Central Vietnam and its effects on their spring migration to China. *Bulletin of Entomological Research*, 107 (3), 369-381. https://doi.org/10.1017/S0007485316001024

Hu G., *et al.*, 2025. The East Asian insect flyway: Geographical and climatic factors driving migration among diverse crop pests. *Annu. Rev. Entomol.*, 70 (1), 1-22. https://doi.org/10.1146/annurev-ento-012524-124018

Huang J., *et al.*, 2024. Massive seasonal high-altitude migrations of nocturnal insects above the agricultural plains of East China. *Proc. Natl Acad. Sci. USA*, 121 (18), e2317646121. https://doi.org/10.1073/pnas.2317646121

Huestis D.L., *et al.*, 2019. Windborne long-distance migration of malaria mosquitoes in the Sahel. *Nature*, 574 (7778), 404-408. https://doi.org/10.1038/s41586-019-1622-4

IPBES, 2023. Thematic assessment report on invasive alien species and their control of the intergovernmental science-policy platform on biodiversity and ecosystem services. Roy H.E., *et al.*, eds. IPBES secretariat, Bonn, Germany. https://doi.org/10.5281/zenodo.7430682

Irwin M.E., *et al.*, 1988. Long-range aerial dispersal of cereal aphids as virus vectors in North America. *Philos. Trans. R. Soc. B Biol. Sci.*, 321 (1207), 421-446. https://doi.org/10.1098/rstb.1988.0101

Isard S.A., *et al.*, 1990. Vertical distribution of Aphids (Homoptera: Aphididae) in the planetary boundary layer. *Environ. Entomol.*, 19 (5), 1473-1484. https://doi.org/10.1093/ee/19.5.1473

Jacquet S., *et al.*, 2016. Range expansion of the Bluetongue vector, *Culicoides imicola*, in continental France likely due to rare wind-transport events. *Sci. Rep.*, 6 (1), 27247. https://doi.org/10.1038/srep27247

Jeffries D.L., *et al.*, 2013. Characteristics and drivers of high-altitude ladybird flight: Insights from vertical-looking entomological radar. *PLoS ONE*, 8 (12), e82278. https://doi.org/10.1371/journal.pone.0082278

Jia H., *et al.*, 2022. Windborne migration amplifies insect-mediated pollination services. *eLife*, 11e76230. https://doi.org/10.7554/eLife.76230

Johnson C.G., 1969. *Migration and dispersal of insects by flight*, London, Methuen & Co. Ltd., 798 p.

Jourdain F., *et al.*, 2012. The moth *Hylesia metabus* and French Guiana lepidopterism: Centenary of a public health concern. *Parasite*, 19 (2), 117-128. https://doi.org/10.1051/parasite/2012192117

Kennedy J.S., 1985. Migration, behavioral and ecological. *Contributions in Marine Science Supplement*, 275-26.

Kim K.S., Sappington T.W., 2006. Molecular genetic variation of boll weevil populations in North America estimated with microsatellites: Implications for patterns of dispersal. *Genetica*, 127 (1-3), 143-161. https://doi.org/10.1007/s10709-005-2673-z

Kim K.S., Sappington T.W., 2013. Population genetics strategies to characterize long-distance dispersal of insects. *Journal of Asia-Pacific Entomology*, 16 (1), 87-97. https://doi.org/10.1016/j.aspen.2012.11.004

Kling M.M., Ackerly D.D., 2020. Global wind patterns and the vulnerability of wind-dispersed species to climate change. *Nature Climate Change*, 10 (9), 868-875. https://doi.org/10.1038/s41558-020-0848-3

Koralewski T.E., *et al.*, 2021. Modeling the dispersal of wind-borne pests: Sensitivity of infestation forecasts to uncertainty in parameterization of long-distance airborne dispersal. *Agric. For. Meteorol.*, 301-302, 108357. https://doi.org/10.1016/j.agrformet.2021.108357

Kutsch W., *et al.*, 2002. Flight capability and flight motor pattern in a sedentary South African grasshopper, *Phymateus morbillosus* – a comparison with migratory species. *Physiological Entomology*, 27 (1), 39-50. https://doi.org/10.1046/j.1365-3032.2002.00267.x

Lancaster J., Downes B.J., 2017. Dispersal traits may reflect dispersal distances, but dispersers may not connect populations demographically. *Oecologia*, 184 (1), 171-182. https://doi.org/10.1007/s00442-017-3856-x

Lander T.A., *et al.*, 2014. Reconstruction of a windborne insect invasion using a particle dispersal model, historical wind data, and Bayesian analysis of genetic data. *Ecol. Evol.*, 4 (24), 4609-4625. https://doi.org/10.1002/ece3.1206

Lefèvre T., *et al.*, 2022. The ecological significance of arthropod vectors of plant, animal, and human pathogens. *Trends Parasitol.*, 38 (5), 404-418. https://doi.org/10.1016/j.pt.2022.01.004

Leitch K.J., *et al.*, 2021. The long-distance flight behavior of *Drosophila* supports an agent-based model for wind-assisted dispersal in insects. *Proc. Natl Acad. Sci. USA,* 118 (17), e2013342118. https://doi.org/10.1073/pnas.2013342118

Lorenz M.W., 2007. Oogenesis-flight syndrome in crickets: Age-dependent egg production, flight performance, and biochemical composition of the flight muscles in adult female *Gryllus bimaculatus*. *J. Insect Physiol.*, 53 (8), 819-832. https://doi.org/10.1016/j.jinsphys.2007.03.011

Lounibos L.P., 2002. Invasions by insect vectors of human disease. *Annu. Rev. Entomol.*, 47 (1), 233-266. https://doi.org/10.1146/annurev.ento.47.091201.145206

Loxdale H.D., *et al.*, 1993. The relative importance of short- and long-range movement of flying aphids. *Biol. Rev.*, 68 (2), 291-311. https://doi.org/10.1111/j.1469-185X.1993.tb00998.x

Mazzi D., Dorn S., 2012. Movement of insect pests in agricultural landscapes. *Ann. Appl. Biol.*, 160 (2), 97-113. https://doi.org/10.1111/j.1744-7348.2012.00533.x

Mikkola K., 2003. The Red Admiral butterfly (*Vanessa atalanta*, Lepidoptera: Nymphalidae) is a true seasonal migrant: An evolutionary puzzle resolved? *Eur. J. Entomol.*, 100 (4), 625-626. https://doi.org/10.14411/eje.2003.091

Morris C.E., *et al.*, 2022. One Health concepts and challenges for surveillance, forecasting, and mitigation of plant disease beyond the traditional scope of crop production. *Plant Pathology*, 71 (1), 86-97. https://doi.org/10.1111/ppa.13446

Osborne J.L., *et al.*, 2002. Monitoring insect dispersal: Methods and approaches. *In*: Bullock J.M., *et al.*, eds, *Dispersal Ecology*, Cambridge University Press, 24-49.

Otuka A., *et al.*, 2019. Possible domestic dispersal of *Bactrocera dorsalis* during 2015 occurrence on the small islands of south-western Japan. *J. Appl. Entomol.*, 143 (5), 556-565. https://doi.org/10.1111/jen.12598

Parlin A.F., *et al.*, 2023. The cost of movement: Assessing energy expenditure in a long-distant ectothermic migrant under climate change. *J. Exp. Biol.*, 226 (21), jeb245296. https://doi.org/10.1242/jeb.245296

Pedgley D.E., 1993. Managing migratory insect pests—a review. *Int. J. Pest Manage.*, 39 (1), 3-12. https://doi.org/10.1080/09670879309371751

Pretorius I., *et al.*, 2023. In the wind: Invasive species travel along predictable atmospheric pathways. *Ecol. Appl.*, 33 (3), e2806. https://doi.org/10.1002/eap.2806

Renault D., 2020. A Review of the phenotypic traits associated with insect dispersal polymorphism, and experimental designs for sorting out resident and disperser phenotypes. *Insects*, 11 (4), 214. https://doi.org/10.3390/insects11040214

Rennie S.J., 2014. Common orientation and layering of migrating insects in southeastern Australia observed with a Doppler weather radar: Common orientation of insects observed with a Doppler weather radar. *Meteorological Applications*, 21 (2), 218-229. https://doi.org/10.1002/met.1378

Reppert S.M., De Roode J.C., 2018. Demystifying Monarch butterfly migration. *Current Biology*, 28 (17), R1009-R1022. https://doi.org/10.1016/j.cub.2018.02.067

Reynolds D.R., *et al.*, 2006. The migration of insect vectors of plant and animal viruses. *Adv. Virus Res.*, 67, 453-517. https://doi.org/10.1016/S0065-3527(06)67012-7

Reynolds A.M., *et al.*, 2007. Ballooning dispersal in arthropod taxa: Conditions at take-off. *Biol. Lett.*, 3 (3), 237-240. https://doi.org/10.1098/rsbl.2007.0109

Reynolds A.M., *et al.*, 2016. Orientation in high-flying migrant insects in relation to flows: Mechanisms and strategies, *Philos. Trans. R Soc. Lond. B Biol. Sci.*, 371 (1704), 20150392. https://doi.org/10.1098/rstb.2015.0392

Reynolds D.R., *et al.*, 2017. Riders on the wind: The aeroecology of insect migrants. *In:* Chilson P.B., *et al.*, eds, *Aeroecology*, Springer International Publishing, 145-178. https://doi.org/10.1007/978-3-319-68576-2_7

Rezza G., 2014. Dengue and chikungunya: Long-distance spread and outbreaks in naïve areas. *Pathogens and Global Health*, 108 (8), 349-355. https://doi.org/10.1179/2047773214Y.0000000163

Ricci C., *et al.*, 2005. Migratory flight and pre-diapause feeding of *Coccinella septempunctata* (Coleoptera) adults in agricultural and mountain ecosystems of Central Italy. *Eur. J. Entomol.*, 102 (3), 531-538. https://doi.org/10.14411/eje.2005.076

Richardson C.H., Nemeth D.J., 1991. Hurricane-borne African Locusts (*Schistocerca gregaria*) on the Windward Islands. *GeoJournal*, 23 (4), 349-357. https://doi.org/10.1007/BF00193608

Roy H.E., Brown P.M.J., 2015. Ten years of invasion: *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Britain. *Ecological Entomology*, 40 (4), 336-348. https://doi.org/10.1111/een.12203

Sánchez-Bayo F., Wyckhuys K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8-27. https://doi.org/10.1016/j.biocon.2019.01.020

Sappington T.W., 2018. Migratory flight of insect pests within a year-round distribution: European corn borer as a case study. *J. Integr. Agric.*, 17 (7), 1485-1505. https://doi.org/10.1016/S2095-3119(18)61969-0

Satterfield D.A., *et al.*, 2020. Seasonal insect migrations: Massive, influential, and overlooked. *Front. Ecol. Environ.*, 18 (6), 335-344. https://doi.org/10.1002/fee.2217

Service M.W., 1997. Mosquito (Diptera: Culicidae) dispersal—The long and short of it. *J. Med. Entomol.*, 34 (6), 579-588. https://doi.org/10.1093/jmedent/34.6.579

Shipilina D., *et al.*, 2024. Gene expression responses to environmental cues shed light on components of the migratory syndrome in butterflies. *bioRxiv*, 2024.07.17.602486. https://doi.org/10.1101/2024.07.17.602486

Siljamo P., *et al.*, 2020. Do atmospheric events explain the arrival of an invasive ladybird (*Harmonia axyridis*) in the UK? *PLOS ONE*, 15 (1), e0219335. https://doi.org/10.1371/journal.pone.0219335

Sloggett J.J., Weisser W.W., 2002. Parasitoids induce production of the dispersal morph of the pea aphid, *Acyrthosiphon pisum*. *Oikos*, 98 (2), 323-333. https://doi.org/10.1034/j.1600-0706.2002.980213.x

Solbreck C., Sillén-Tullberg B., 1990. Population dynamics of a seed feeding bug, *Lygaeus Equestris*. 1. Habitat patch structure and spatial dynamics. *Oikos*, 58 (2), 199-209. https://doi.org/10.2307/3545427

Soubeyrand S., *et al.*, 2024. Building integrated plant health surveillance: A proactive research agenda for anticipating and mitigating disease and pest emergence. *CABI Agric. Biosci.*, 5 (1), 72. https://doi.org/10.1186/s43170-024-00273-8

Srygley R.B., Dudley R., 2007. Optimal strategies for insects migrating in the flight boundary layer: Mechanisms and consequences. *Integr. Comp. Biol.*, 48 (1), 119-133. https://doi.org/10.1093/icb/icn011

Stefanescu C., *et al.*, 2013. Multi-generational long-distance migration of insects: Studying the painted lady butterfly in the Western Palaearctic. *Ecography*, 36 (4), 474-486. https://doi.org/10.1111/j.1600-0587.2012.07738.x

Strona G., *et al.*, 2020. Small world in the real world: Long distance dispersal governs epidemic dynamics in agricultural landscapes. *Epidemics*, 30, 100384. https://doi.org/10.1016/j.epidem.2020.100384

Suchan T., *et al.*, 2024. A trans-oceanic flight of over 4,200 km by painted lady butterflies. *Nat. Comm.*, 15 (1), 5205. https://doi.org/10.1038/s41467-024-49079-2

Sun B., *et al.*, 2020. Nocturnal dispersal flight of crickets: Behavioural and physiological responses to cool environmental temperatures. *Functional Ecology*, 34 (9), 1907-1920. https://doi.org/10.1111/1365-2435.13615

Suter R.B., 1999. An aerial lottery: The physics of ballooning in a chaotic atmosphere. *The Journal of Arachnology*, 27, 281-293.

Talavera G., Vila R., 2017. Discovery of mass migration and breeding of the painted lady butterfly *Vanessa cardui* in the Sub-Sahara: The Europe-Africa migration revisited. *Biological Journal of the Linnean Society*, 120 (2), 274-285. https://doi.org/10.1111/bij.12873

Talavera G., *et al.*, 2023. The Afrotropical breeding grounds of the Palearctic-African migratory painted lady butterflies (*Vanessa cardui*). *Proc. Natl Acad. Sci. USA,* 120 (16), e2218280120. https://doi.org/10.1073/pnas.2218280120

Taylor L.R., 1974. Insect migration, flight periodicity and the boundary layer. *Journal of Animal Ecology*, 43 (1), 225-238. https://doi.org/10.2307/3169

Wang H.-H., *et al.*, 2019. Integrated modelling of the life cycle and aeroecology of wind-borne pests in temporally-variable spatially-heterogeneous environment. *Ecological Modelling*, 399, 23-38. https://doi.org/10.1016/j.ecolmodel.2019.02.014

Wang X., *et al.*, 2014. The locust genome provides insight into swarm formation and long-distance flight. *Nat. Comm.*, 5 (1), 2957. https://doi.org/10.1038/ncomms3957

Warfvinge K., *et al.*, 2017. The power–speed relationship is U-shaped in two free-flying hawkmoths (*Manduca sexta*). *J. R. Soc. Interface*, 14 (134), 20170372. https://doi.org/10.1098/rsif.2017.0372

Weisser W.W., *et al.*, 1999. Predator-induced morphological shift in the pea aphid. *Proc. R. Soc. B Biol. Sci.*, 266 (1424), 1175-1181. https://doi.org/10.1098/rspb.1999.0760

Wikelski M., *et al.*, 2006. Simple rules guide dragonfly migration. *Biol. Lett.*, 2 (3), 325-329. https://doi.org/10.1098/rsbl.2006.0487

Wiklund C., Friberg M., 2022. Testing the migration syndrome: Comparative fecundity of migratory and non-migratory nymphaline butterflies. *Ecological Entomology*, 47 (6), 1061-1067. https://doi.org/10.1111/een.13195

Wotton K.R., *et al.*, 2019. Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology*, 29 (13), 2167-2173.e5. https://doi.org/10.1016/j.cub.2019.05.036

Wu Q.-L., *et al.*, 2018. An advanced numerical trajectory model tracks a corn earworm moth migration event in Texas, USA. *Insects*, 9 (3), 115. https://doi.org/10.3390/insects9030115

Yaro A.S., *et al.*, 2022. Diversity, composition, altitude, and seasonality of high-altitude windborne migrating mosquitoes in the Sahel: Implications for disease transmission. *Front Epidemiol.*, 2, 1001782. https://doi.org/10.3389/fepid.2022.1001782

Zera A.J., Denno R.F., 1997. Physiology and ecology of dispersal polymorphism in insects. *Annu. Rev. Entomol.*, 42 (1), 207-230. https://doi.org/10.1146/annurev.ento.42.1.207

Zimmerman E.C., 1948. *Insects of Hawaii. Vol. V. Homoptera: Sternorhyncha. Superfamily Psylloidea*, University of Hawaii Press, Honolulu, 464 p.

Chapter 10

Glacial archives of ancient atmospheres and aerobiota

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Bioaerosols are small (~10-100,000 nm) airborne particulates or droplets that are comprised of viruses, microbes (i.e., fungi, protozoa, algae, bacteria, and archaea), spores, and pollen, as well as various forms of biogenic material (Xie *et al.*, 2021). They are generated through natural and anthropic processes, such as sea spray-mediated processes at the ocean surface, dust storms, wastewater treatment, and agriculture (Bulski, 2020; Kumar *et al.*, 2024; Mohaimin *et al.*, 2023; Sánchez-Monedero *et al.*, 2008). The dynamics of bioaerosol transmission are influenced by atmospheric currents and climatic events, mechanisms of formation of aerosols, physical properties of particulates or colloids, and the nature of their biological component. Natural events, such as hurricanes, dust storms, or wildfires, increase amounts of particulate matter and bioaerosols in the atmosphere (Alsved *et al.*, 2020) as described in the chapters of Section 1. Moreover, bioaerosols have important roles in biological dispersal, biogeochemical cycling, and air quality, and they can also play direct roles in hydrologic cycling. Vertical mixing in the atmosphere transports bioaerosols high into the troposphere, and even into the stratosphere (Bryan *et al.*, 2019), allowing for the possibility of transport over intercontinental distances. The local to global dispersal of bioaerosols via atmospheric transport allows many organisms to utilize atmospheric travel as a key component of their life cycle.

Human activities are driving unprecedented environmental, climatic, and ecological changes, including global warming, biodiversity loss, and resource depletion. The effects of urbanization, industrialization, and agriculture on sources and distributions on bioaerosols is not well known, nor are the full implications to the ecosystems of deposition. Part of the challenge with this topic is the pervasiveness and scale of anthropic influence on the modern atmosphere and environment, complicating our ability to know the baseline conditions of a natural state. Alongside impacts on atmospheric aerosols and greenhouse gas composition, human activities affect microbial communities, which are sensitive indicators of climate and environmental change. Given the changes that are currently underway, there is critical need to know how organisms and ecosystems will respond to climate and landscape changes in the decades to come. To make informed predictions for ecosystems in the future, we must better understand the changes that accompanied climate shifts in the past.

There are a number of geological materials that archive biological particles and provide information on aerosols distributed in past atmospheres. For example, studies of peat have been valuable for tracing atmospheric composition over time, and cores from peat bogs have been used to enumerate levels of atmospheric mercury, cadmium, and platinum, as well as carbon sequestration during past climate fluctuations (Aubert *et al.*, 2006; Madsen, 1981; Rauch *et al.*, 2004; Shotyk *et al.*, 2016; Stewart and Fergusson, 1994). More recently, peat cores have been used to assess levels of atmospheric microplastics, an emerging pollutant (Allen *et al.*, 2021). Loess is another type of paleoclimatic record largely composed of stratified sediments of windborne silt that can contain millennial timescales of atmospheric deposition (Muhs *et al.*, 2014). Loess records provide clear indicators of glacial versus interglacial periods, as the extent of soil formation in loess sediments is greatly reduced during glacial stages. Interglacial periods coincide with increased abundance and diversity in the loess microbiome, such that microbial growth can be correlated with interglacial climate (Frindte *et al.*, 2020). Magnetism of

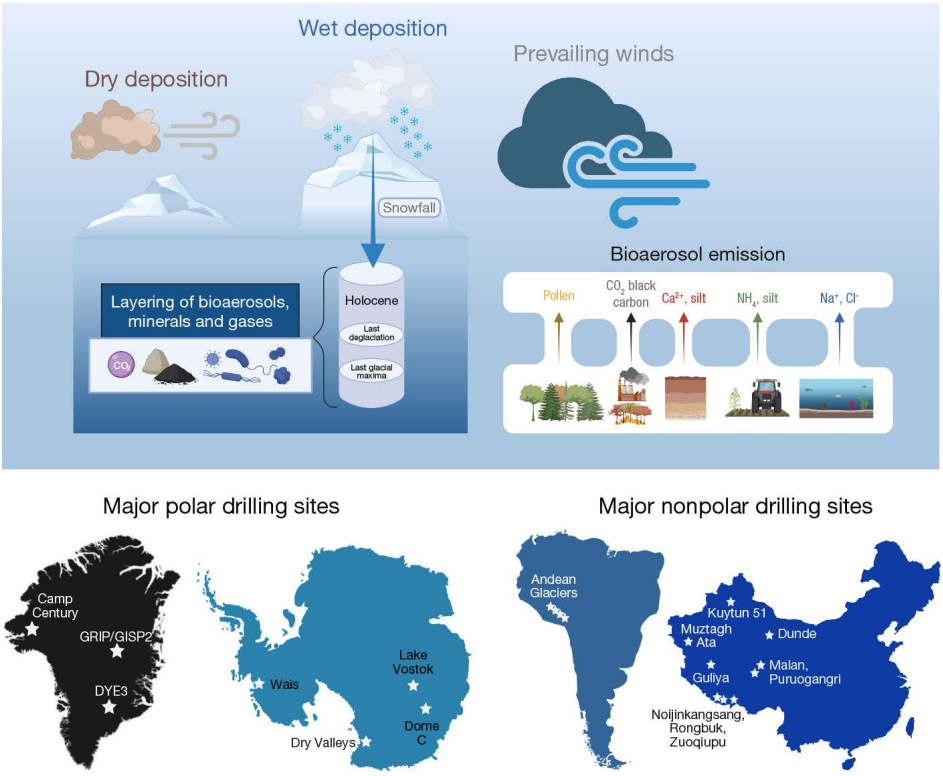

Figure 10.1. The various sources of bioaerosols (top schematic) –pollen from vegetation, emissions from forest fires and fossil fuel burning, dust vectors from desert regions, and oceanic disturbances– and glaciers that have been explored as sinks of these bioaerosols (lower schematic).

These bioaerosols are deposited in glacial ice through wet deposition (e.g., snow, ice) and dry deposition (e.g., erosion, dust storms). The patterns of bioaerosols, minerals, and gases immured in englacial ice allows us to characterize major climate cycles of the past, such as glacial maxima and retreat. The lower schematic gives relative positions of major glaciers that have been cored and separated into polar glaciers found in Greenland and Antarctica, and nonpolar glaciers found mainly in South America and the Tibetan Plateau. Note that Guliya glacier resembles a polar glacier, despite its equatorial locale (Zhong *et al.*, 2021).

loess soils can also provide information about moisture and redox conditions that are generally associated with wet periods (Lauer *et al.*, 2017). Peat microbial communities have been investigated extensively; however, active *in situ* growth and percolation do not allow faithful reconstructions of the ancient microflora composition (Fracasso *et al.*, 2024). Similarly, loess also contains a mixture of modern and ancient microbiota, making it challenging to differentiate historical deposition sources.

Though advances in ancient DNA research have assisted with tracking the vintage of microbiota detected in peat and loess ecosystems (Fracasso *et al.*, 2024; Frindte *et al.*, 2020), glacial ice paleorecords provide a superior alternative that circumvent issues of ancient provenance. Ice cores that have been drilled from a global array of glaciers represent the most extensively studied natural archive for investigations of the composition of past atmospheres. This is primarily due to the processes that form glacial ice, which preserve material in a chronological sequence over timeframes that can be in excess of a million years. As the type and concentration of microbes and other biological materials (e.g., pollen) in the ice are dependent on environmental conditions at the time of deposition, they serve as important palaeoecological markers to indicate shifts related to past climate events.

In this chapter, we discuss how bioaerosols are involved with and captured during the formation of snow and glacial ice, research on these materials to infer properties of the atmosphere and environments of the past, and the recent advances that have allowed the biological content of ancient ice to be fully realized. In addition to providing an overview of the biological signals preserved in glacial ice and efforts to trace microbial deposition in glaciers, we also aim to illuminate the potential for glacial ice archives to reveal how the atmosphere and ecosystems responded to past climatic shifts. The wealth of biological information contained within glacial ice paleorecords provides opportunities to infer the properties of bioaerosols over geological timeframes and to project ecosystem responses to future climate changes. Figure 10.1 summarizes the various sources of bioaerosols and the geographical locations of the glaciers that have been explored to examine the fate of their voyages.

⏩ Role and fate of aerosols in snowfall

The importance of snow for Earth's energy balance, hydrologic cycling, and ecosystems worldwide is widely recognized. Snowfall accumulation is prevalent at high-latitudes and in mountainous locations, including the Tropics (e.g., Andes). In temperate regions, seasonal snowpack regulates climate, supports freshwater resources, and has vital socioeconomic functions (López-Moreno *et al.*, 2024). A key feature of snow formation and deposition is that the process captures environmental information allowing climatic, atmospheric, and biological conditions at the time of deposition to be inferred. As unmanned atmospheric observatories, investigations of snow have provided a pragmatic approach to examine the spatial and temporal characteristics of meteorologically relevant bioaerosols (Christner *et al.*, 2008b; Aho *et al.*, 2020; Joyce *et al.*, 2019) and microbes co-transported in Saharan dust plumes (Meola *et al.*, 2015; Weil *et al.*, 2017). When annual layers of snow accumulate season after season and are compressed into glacial ice, there is the potential to peer far back into the past. In the case of the oldest glacial ice from Antarctica, it is possible to examine material as old as 1.5 to 3 million years (Chung *et al.*, 2024; Peterson *et al.*, 2024).

As moist air rises in the atmosphere, it undergoes adiabatic cooling that condenses water vapor on an aerosol type called a cloud condensation nuclei, generating the micrometer-sized water droplets that make up clouds. In addition to water, the cloud aerosols are also comprised of organic compounds, dust, sea salt, anthropogenic pollutants (e.g., sulfates and nitrates), and a variety of microbes. Research on the microbes present in cloud droplets has shown their capacity to metabolize and biogeochemically alter cloud water chemistry, as described in Chapter 6. There are also indications that certain bioaerosols may play active roles in the meteorological processes that produce precipitation. Most snowfall is produced by mixed-phase clouds that contain a combination of both liquid water droplets and ice particles. At subzero temperature and conditions of saturated relative humidity, ice particles in mixed-phase clouds grow at the expense of vapor supplied from supercooled liquid water droplets. This, together with a process that freezes the liquid droplets directly, is responsible for the initial steps that lead to the generation of ice-based precipitation. The reason that not all the water droplets in a cloud are frozen is that the formation of ice is highly dependent on the presence of a relatively rare cloud aerosol that greatly enhances freezing (Pruppacher and Klett, 2010).

Spontaneous freezing of pure liquid water does not occur above a temperature of approximately –36ºC. Ice crystals that form at warmer subzero temperatures are assisted by ice nucleating particles (INPs) in a process called heterogeneous nucleation (Vali, 1995). INPs function by providing surfaces for water molecules to bind and organize into a crystalline structure, which lowers the energy barrier for ice formation. The efficacy of a particle to serve as an INP depends on its composition, morphology, and size, and a diverse range of particles can serve as INPs (Szyrmer and Zawadzki, 1997). Abundant mineral dust aerosols in the atmosphere are believed to be the dominant type of INP responsible for ice formation in clouds. However, since mineral INPs initiate freezing at temperatures well below –15ºC, direct observation of ice in clouds warmer than this has been difficult to explain (DeMott and Prenni, 2010; Phillips *et al.*, 2013). In the late 1950s, atmospheric scientists began to explore INPs active at temperatures > –10ºC through analysis of snow, rain, and hailstones samples. Despite these efforts, the sources of the warm temperature ice nucleating material remained elusive for years.

Pioneering work in the 1970s demonstrated that the most active naturally occurring INPs are bacterial in origin. This was initially observed in the phytopathogenic bacterium *Pseudomonas syringae*, where some strains have been shown to be capable of catalyzing freezing at temperatures near –2°C (Maki *et al.*, 1974). *P. syringae* remains the most well characterized and recognized ice nucleating bacterium, but the homologous phenotype is also distributed in other closely related Gammaproteobacteria including *P. viridiflava, P. fluorescens, Pantoea agglomerans,* and *Xanthomonas campestris.* Subsequent research has also documented ice nucleating activity in a gram-positive bacterial species (Failor *et al.*, 2017), as well as fungi (e.g., *Fusarium avenaceum*), algae (e.g., *Chlorella minutissima* and *Thalassiosira pseudonana*; Knopf *et al.,* 2011), and birch pollen (Pummer *et al.*, 2012). In particular, *P. syringae* (Lindemann *et al.*, 1982; Morris *et al.*, 2008; Sands *et al.*, 1982) and *F. avenaceum* (Amato *et al.*, 2007) can be readily detected in precipitation, atmospheric aerosols, and cloud water.

The discovery of plant-associated bacteria capable of performing ice nucleation coupled with their presence in precipitation and at altitudes of several kilometers

above the surface (Jayaweera and Flanagan, 1982; Sands *et al.*, 1982) served as the motivation for a hypothesis called bioprecipitation. This concept, proposed by David Sands, argued for a feedback process that links plants in surface environments to atmospheric phenomena responsible for snow and rain (Morris *et al.*, 2008). Given the enormous numbers of microorganisms on leaf surfaces globally (10^{24} to 10^{26} cells; Morris and Kinkel, 2002) and large populations of ice-nucleating bacteria (up to 10^5 ice-nucleating bacteria/cm^2 of leaf area; Lindow *et al.*, 1978), global vegetation represents a large terrestrial source of biological INPs. Reports of elevated biological INPs in phytoplankton-rich ocean waters (Schnell and Vali, 1975) and sourced from their exudates (Wilson *et al.*, 2015) also imply that marine ecosystems are substantial biological INP sources to the atmosphere. Data on the abundance of biological INPs in snow (Christner *et al.*, 2008a, 2008b; Morris *et al.*, 2008) and rain (Joyce *et al.*, 2019) confirm their widespread distributions in the atmosphere. However, modeling studies that have evaluated the role of biological INPs in precipitation have reached disparate conclusions. While some studies imply biological INPs are at concentrations too low to be significant on a global scale (Hoose *et al.*, 2010), others have found evidence that they are potentially important (Phillips *et al.*, 2009; Tobo *et al.*, 2013). One of the major challenges in assessing the effects of biological INPs on precipitation formation is a lack of observations for their in-cloud concentrations, forcing numerical modeling efforts to base their studies on very limited data.

While full understanding of the meteorological role that microbial aerosols play requires further research and remains a topic fertile for discovery, it is evident that rain and snow serve as a mechanism that deposits aerosolized bacterial and fungal assemblages to the surface. Unsurprisingly, the compositions of microbial assemblages in wet deposition are linked to site, season, and air mass history. It is interesting to note that bacterial composition in precipitation has been found to be more strongly associated with macroscale-driven storm characteristics, whereas fungal assemblages were associated with mescoscale drivers (Aho *et al.*, 2020). Due to enhanced scavenging from the atmosphere during precipitation and gravitational effects on larger fungal spores and organisms, their distribution range appears more limited in comparison to prokaryotic cells that possess smaller aerodynamic diameters. Ice nucleation activity may enhance the efficiency at which an aerosol is removed from the atmosphere during precipitation, but all aerosols are subject to in- and below-cloud scavenging. Scavenging by a rain drop occurs through several distinct mechanisms (Moore *et al.*, 2020), but it also occurs as snowflakes form and fall to the ground (Kyrö *et al.*, 2009; Paramonov *et al.*, 2011; Zhang *et al.*, 2013). Where freshly deposited, seasonal snowpacks, or even multi-year sequences of snow are available, analysis of impurity contents provide ripe opportunities for study designs that accommodate time-integrated sampling over wide spatial coverage without the need for maintaining specialized and expensive sampling equipment.

⏩ Ice cores and their microbiological contents

Physical, chemical, and biological data collected from glacial ice cores, including long term paleorecords of atmospheric gas compositions, have been invaluable for reconstructing Earth's climate history. The deepest and oldest ice core records have been obtained by drilling projects in Greenland and Antarctica (see Jouzel (2013)

for a historical perspective). The first long ice core record was obtained at Vostok Station in East Antarctica, where several cores were drilled by the Russians during the 1980s. The longest record (5G ice core) was completed in the early 1990s at a depth of 3,623 m through a joint Russian, French, and American effort. The 420,000 years of paleoclimatic record from Vostok 5G is historically significant because it contains four full glacial-interglacial cycles and provided the first evidence of the close relationship between greenhouse gas concentrations and global temperatures (Petit *et al.*, 1999). More recently, drilling at Dome C in East Antarctica by a European consortium and at Dome Fuji (Dome F) have extended these records, with the oldest ice in excess of 800,000 years (Bazin *et al.*, 2013).

Several deep ice coring efforts have also been done in Greenland, such as the European Greenland Ice core Project (GRIP) and the American Greenland Ice Sheet Project 2 (GISP2) (Mayewski *et al.*, 1994). Both projects drilled near Summit in central Greenland and provide 120,000 years of paleorecords for the Arctic and northern hemisphere that date to the last interglacial period (Eemian). To date, the longest continuous record from Greenland was obtained at the NEEM (North Greenland Eemian) drilling site, which recovered a 2,537 m core spanning 128,500 years (Popp *et al.*, 2014). Ice core records from Greenland, Antarctica, and the Tibetan Plateau (Thompson *et al.,* 1997) have been used to reconstruct the last glacial-interglacial cycle and provide perspective on the how the atmosphere, climate, and environment were modified by the strongest of all natural perturbations – a glacial event.

The vast size of the Antarctic and Greenland ice sheets affects local (as well as global) weather patterns, and within their remote interiors, there are few local aerosol sources. This is very different from alpine glaciers at lower latitudes that extend into the Tropics, which are in close proximity to major ecosystems and have been shown to be highly sensitive in recording high frequency climatic perturbations and anthropogenic inputs. Pioneering efforts led by Lonnie Thompson in the 1970s to drill and recover a 1,500-year-old core from the Quelccaya Ice Cap in Peru were the first to demonstrate the value of ice core records from the Tropics (Thompson, 2017). This core provided data during the Little Ice Age, recording local climate fluctuations for the Southern hemisphere during the Late Holocene and signals attributed to the activities of ancient Andean civilizations. Other ice core records have since been obtained from the Andes (Huascaran, Peru and Sajama, Bolivia) that extend observations to the Last Glacial Stage (Vuille *et al.*, 2008). Multiple non-polar ice cores have also been obtained from regions in the Himalayas as well as East Africa (Kilimanjaro, Tanzania; Thompson *et al.*, 2002). The range of ice core records studied to date has provided critical data on past temperature, precipitation, and atmospheric composition from regions in the Tropics to high latitudes.

Mineral and biological impurities immured in the ice represent material that was aerosolized from a variety of sources (e.g., deserts, forests, volcanic eruptions, or industrial activity). Sabit Abyzov (1998) was the first to explore the potential for microbes to be preserved in ancient ice through isolation of a variety of bacteria, yeast, and fungi from ice cores that were collected and sampled at the remote Vostok station. This work was extended to a range of polar and non-polar ice cores (Christner *et al.*, 2000), which showed many hardy bacterial species common among sites that were capable of widespread atmospheric distribution through precipitation. Atmospheric dust loading

positively correlates with culturable diversity in glacial ice, supporting that a key mechanism of transport is through cellular associations with aerosolized particulates (Christner *et al.*, 2000; Knowlton *et al.*, 2013; Miteva *et al.*, 2009; Santibáñez *et al.*, 2018; Yao *et al.*, 2006; Zhang *et al.*, 2007). The psychrophiles that have been characterized from glacial ice are generally those from four major phyla, Actinobacteria, Proteobacteria (Alphaproteobacteria and Gammaproteobactera), Bacteroidetes, and Firmicutes (Junge *et al.*, 2011; Miteva, 2008; Shen *et al.*, 2018).

Many of the viable species cultured from ice cores have adaptations that would assist with survival in the atmosphere and glacial ice. Gram-positive spore formers, such as *Bacillus* and *Paenibacillus,* have been isolated from Greenland, as well as cores from the Malan glacier of the Tibetan Plateau (Christner *et al.*, 2000; Knowlton *et al.*, 2013; Miteva *et al.*, 2009; Xiang *et al.*, 2004; Yao *et al.*, 2006). *Bacillus* have been consistently isolated from both Greenlandic and Antarctic ice, however with different lineages observed between poles (Knowlton *et al.*, 2013). Nonsporulating gram positives such as *Arthrobacter* and *Actinobacteria* (e.g., *Micrococcus*) are similarly ubiquitous. Other common genera include *Microbacterium, Brachybacterium, Brevibacterium,* and *Methylobacterium.* A recent study of the Guliya ice core found an abundance of *Microbacteriaecae,* the *Actinobacteria* family that includes the psychrophilic genus *Cryobacterium* (Zhong *et al.*, 2021). *Cryobacterium* has been extensively observed in the cryosphere and is a model group for the study of microbial cold adaptation (Liu *et al.*, 2019, 2023). Whole-genome sequencing of *Cryobacterium* strains isolated from glacial ice found an accumulation of stress-resistance genes relative to *Cryobacterium mesophilium,* its temperate relative (Liu *et al.*, 2020). *Flavobacteriaceae* are also common taxa in Antarctic and Tibetan ice cores (Christner *et al.*, 2000; Liu *et al.*, 2019; Zhong *et al.*, 2021). Some *Flavobacteriaceae* strains have shown increased levels and diversity of branched unsaturated fatty acids in their membranes, which may contribute to their cold tolerance (Králová, 2017), while others produce ice binding proteins that inhibit ice recrystallization and protect cells during freezing and thawing (Achberger, 2011).

Fungi in glacial ice have largely been studied in the context of biodiversity, however fungi and their spores are in some cases the main culturable component of ancient ice (Knowlton *et al.*, 2013). Basidomycetous yeasts predominate in glacial ecosystems, however geographic location and deposition environment seems to have a significant impact on their distribution (Duo Saito *et al.*, 2018; Ma *et al.*, 1999; Perini *et al.*, 2021). Some cosmopolitan fungi and yeast, including *Rhodotorula, Cryptococcus*, *Cladosporum, Penicillium,* and *Aspergillus,* have been cultured from polar and nonpolar glaciers worldwide (de Menezes *et al.*, 2020; Ma *et al.*, 1999; Perini *et al.*, 2021; Singh *et al.*, 2013; Tsuji *et al.*, 2022). Small subunit rRNA sequencing and metagenomics alongside culturing efforts have identified many fungal species that are unique to glacial ice. Whether these represent ancient species remains unclear (Knowlton *et al.*, 2013; Ma *et al.*, 1999). However, approximately half of the isolates from a large fungal library of glacial meltwater from Greenland and Svalbard could not be identified at the species level, and novel taxa have been retrieved from glacial ice (Perini *et al.*, 2019a, 2019b, 2021). This suggests that some glacial fungi may be unidentified or extinct in other environments. As with psychrophilic bacterial species, fungi of glacial origin are promising reservoirs of bioindustrial activities, including production of secondary metabolites and lipid biogenesis (Amaretti *et al.*, 2010).

Viruses preserved in englacial ice were initially identified in 1999, when RT-PCR sequencing revealed the presence of Tomato mosaic tobamovirus in 500-year-old sections from Greenland's Dye 3 and GISP2 ice cores, demonstrating that glacial ice could maintain stable RNA molecules for extended time periods (Castello *et al.*, 1999). Minimal attention had subsequently been given to glacial ice-preserved viruses until recent studies out of Thompson and Sullivan's group investigated the presence of viral particles deposited in the Guliya glacier on the Tibetan Plateau (Zhong *et al.*, 2021). In their paper, they found that glacial viruses fail to map to known viruses at a higher rate than in other viral metagenomes from environmental samples, suggesting that englacial viruses were evolutionary distinct from contemporary populations. Further, viral abundance could be correlated to host abundance, specifically for *Methylobacterium*-infecting phages, which dominated in the sampling. These data also imply an ecological niche exists for viruses in glacier ice, and led to further investigation of the Guliya ice core, expanding the viral library and linking it to climate data from 160 to 41,000 years ago (Zhong *et al.*, 2024). Though 97% of the ~1,700 taxonomic units identified could not be classified, the results nevertheless support the hypothesis that englacial ice archives ancient viruses that were once dispersed in the atmosphere.

⏩ Ice core research to reconstruct paleoenvironments

While reconstruction of ancient climates is possible at relatively high resolution and confidence, determining the sources of ancient microbial species emitted as aerosols is highly challenging. Source tracing of microorganisms can be informed by mineralogical and ion composition, as well as targeting analyses for specific groups that provide information on source regions (e.g., taxa associated with soil vs. aquatic ecosystems). Another consideration is post-depositional microbial activity, where post-deposition growth and alteration of assemblage structures in the snow may occur (Xiang *et al.*, 2009). This can distort microbial abundances that were originally deposited via aeolian or wet (snow/precipitation) mechanisms, complicating inferences of atmospheric inputs. Importantly, the degree of post-depositional alteration in community structures provides information on environments at the snow surface (Chen *et al.*, 2016) and serves as an indicator of past climatic conditions.

Although sunlight cannot penetrate into deep regions of glacial ice to drive photosynthesis, the liquid veins of ice crystal boundaries contain various compounds, such as ammonia and organic compounds, that could support microbial metabolism within apparently solid ice (Price, 2000; Tung *et al.*, 2006). Analysis of ice core gas anomalies together with preserved DNA and functional metabolic profiling of englacial ice implies that maintenance metabolism, largely relating to DNA repair and amino acid racemization, is sustained (Ahn *et al.*, 2004; Bidle *et al.*, 2007; Buford Price, 2010; Campen *et al.*, 2003; Price, 2007). These data, along with viability of immured microbes over timeframes of hundreds of thousand of years, suggests that some fraction of microbial species demonstrate limited *in situ* metabolic activity. As well, indirect evidence has been provided in support of microbial origins for abnormal concentrations of methane found in the ice core record (Buford Price, 2010; Tung *et al.*, 2005). The question of microbial metabolic acitivty in englacial ice is a difficult experimental problem that remains unresolved. It is clear that microbial growth and activity is greatly reduced in the extreme environment of englacial ice. However, when reconstructing

paleoenvironments, it is important to remember that organisms identified in and cultured from ancient ice may represent the current status of these communities and not a wholly preserved archive of their historical niche and structure.

With respect to source environments for ice core records, there are key differences between those for polar and nonpolar glaciers. Primarily, nonpolar glaciers are in close proximity to local soil and forested ecosystems that are the major sources of aerosols in the atmosphere. The closer proximity of Greenland to land masses in the Northern Hemisphere results in higher amounts of microbial cell deposition than for Antarctica, which has an estimated 16% of the microbial flux relative to Greenland (Price *et al.*, 2009). While local and regional aeolian sources also exist for polar glaciers, the landscapes and soils of extreme environments, such as those in Antarctica, have low productivity and contain much lower cell concentrations than those observed at lower latitudes. In addition, the assemblages deposited in polar snow are less likely to undergo large scale post-depositional microbial growth due to their metabolism being limited by very low temperatures (Santibáñez *et al.*, 2018).

The relationship between climate and glacier microflora varies based on glacier location and type, and most inconsistencies can be explained by regional influences, i.e., maritime vs. continental non-polar glaciers, proximity to anthropogenic inputs, influence of monsoons and Westerlies. For instance, dust concentrations reveal the turbidity of the atmosphere and provide an indication for aridity during the time of deposition. The positive correlation between incident dust with microbial abundances and taxa in deep ice cores was an early observation made for various ice cores (Abyzov *et al.*, 1998; Christner *et al.*, 2000). A study of four portions of the GISP2 record corresponding to varying deposition climates (warm, mild, cool) and dated from 57,000-110,000 years ago confirmed that periods of high aeolian influx resulted in increased bacterial abundance (Miteva *et al.*, 2009). Interestingly, prokaryotic abundance did not correlate with terrestrial non-sea salt Ca^{2+} ions found in cores from Western Antarctica's WAIS (West Antarctic Ice Sheet) Divide (Santibáñez *et al.*, 2018), suggesting that the primary depositional input was not from soil bioaerosols. As opposed to aeolian factors, temperature or seasonality is the most consistent predictor of bacterial abundance in glacier ice. Colder climates of Antarctica and Greenland are characterized by higher aridity and wind intensity, favoring the formation of aerosols containing particulate matter that is co-transported with (or transports) higher abundances and types of bacteria and fungi (Miteva *et al.*, 2009; Santibáñez *et al.*, 2018).

Polar ice cores provide millennial perspectives on temperature fluctuations of bacterial and fungal bioaerosols. In GISP2, there is high correlation of climate variables and microbial abundance in ice from the middle of the Late Pleistocene and the Eemian interglacial/glacial periods, approximately 63,200 years ago (Miteva *et al.*, 2009). The WAIS Divide core records prokaryotic abundance across the Last Glacial Maxima, the Last Deglaciation, and the early Holocene (26,830 to 11,600 years ago), with the glacial maxima corresponding to consistently high bacterial abundances (Miteva *et al.*, 2009; Santibáñez *et al.*, 2018). Molecular analysis of DNA extracted from the Dye 3 core in Greenland, containing ice that predates the Last Interglacial period (~130,000 to 116,000 years ago), showed the region was once home to an ancient coniferous forest (Willerslev *et al.*, 2007). While investigations of the relationship between microbial abundance and climate events in Arctic and Antarctic polar cores is minimal, this is a valuable research area that should be exploited in future.

The drilling and analysis of ice cores from the Tibetan Plateau and other regions in the Himalayas have provided key data to guide hypothesis about microbes as climatic indicators. Several independent studies have confirmed that incidence of particulates correlates with cell density (Chen *et al.*, 2014, 2016; Yao *et al.*, 2006, 2008; Zhang *et al.*, 2007). However, deviations from this phenomenon have been reported in both polar and nonpolar cores, where spikes in bacterial abundance or cell density are not always correlated with Ca^{2+} levels, a proxy for atmospheric dust. In subsections of the 47 m Geladaindong ice core site, located near the headwaters of the Yangtze River, Ca^{2+} concentrations peaked significantly in the 1970s, though this coincided with only a moderate increase in bacterial abundance (Yao *et al.*, 2008). This abnormality was attributed to suppression of post-depositional microbial activity due to relatively low temperatures observed during this period. Similarly, microbial abundances peaked in clean ice sections of the Muztagh Ata and Dunde glaciers, in Western and Eastern-Central China, respectively (Chen *et al.,* 2014). The microbial communities in Dunde, as well as other maritime nonpolar glaciers in Southeastern China, are strongly affected by monsoon cycles. Interestingly, monsoon seasons are reliably associated with lower microbial abundances than pre- and post-monsoon periods, indicating that wet or "clean" deposition contributes fewer deposited bioaerosols than dry periods and aeolian sources (Liu *et al.*, 2016; Mao *et al.*, 2022; Zhang *et al.*, 2007).

Efforts in culturing bacteria from the Malan ice core, a shallow nonpolar glacier in Central China dated from ~1170 to 1999 AD, found that historically lower temperatures corresponded to higher bacterial abundances (Xiang *et al.*, 2004). In contrast, observations from several other nonpolar glaciers show positive correlations between temperature and bacterial or viral abundances, such as Geladaindong and Muztagh Ata (Chen *et al.*, 2016; Yao *et al.*, 2008; Zhong *et al.*, 2024). These discrepancies have been attributed to post-depositional microbial growth during summer months, but they may also be a consequence of Westerly or monsoon incidence on Muztagh Ata and Gelandiandong, respectively. Analysis of the Guliya core demonstrated significant variance in viral community structure with temperature, which was attributed to a combination of both post-depositional host colonization and speciation, as well as influence of aeolian and wet deposition of Westerlies and Indian monsoons (Zhong *et al.*, 2021, 2024).

Bacterial taxa cluster according to ice strata, such that depth/age can serve as a major predictor of microbial variation in an ice core sections. Although similar psychrotolerant taxa are deposited in glacial ice over time, climate shifts influence relative abundances. Analysis of four sections of the Malan ice core from variable climates revealed depth-specific enrichments of Alpha-, Beta- and Gammaproteobacteria as well as members of the Bacteroidota. As well, different species of the same taxa were observed at different depths, suggesting that climate is a driver of speciation. A comparative study of Muztagh Ata and Dunde ice cores found similar species variation within taxa, indicating that geographic location is also a factor in species selection (Chen *et al.*, 2016), likely due to local and regional difference in aerosol sources. The nature and incidence of microbial species also depends on seasonality, where periods of low aeolian influxes and high precipitation correlate to increased incidence of marine microorganisms (Zhang *et al.*, 2007). Prokaryotic abundance has also been linked to periods of oceanic turbulence in the Antarctic, where abundance correlated with levels of sea salt Na^{2+} ions in the WAIS Divide core (Santibáñez *et al.*, 2018).

There are large uncertainties with tracing microbial species to their sources of origin, but advances in metagenomics and increased cataloging of global data in genome databases has improved the reliability of predictions. Correlations between taxa and mineral or biogeochemical data provide starting points for microbial tracing. Isolated bacteria that largely included halotolerant *Bacillus* spp. from GISP2 had previously been identified in the deserts of Southeast China and India, consistent with Greenland's mineral dust primarily originating from Asian deserts. Relatives of marine organisms that were enriched in portions of GISP2 had been previously isolated from the Yellow Sea and coincided with Na^+ and Cl^- concentrations, suggesting microbial sources associated with sea-to-air transfer.

More recently, the use of metagenomic approaches has expanded the toolkit for source tracking and predictions of the influence of past climate on microbiota. Mapping of Operational Taxonomic Units (OTUs) from more recent (~1950-2010) subsections of the monsoon- and westerly-influenced Chinese glaciers Geladaindong, Zuoqiupu, and Noijinkangsang allowed for tracking of 25 to 46% of microbes to their source environments (Liu *et al.*, 2016). In general, northwestern Geladaindong and southwestern Noijinkangsang were dominated by soil- and lake-derived taxa, suggesting that the primary bioaerosol sources were from the Westerlies. Southeastern Zuoqiupu was enriched with marine microorganisms, indicating that the monsoon carrying bioaerosols from the Indian Ocean was the primarily aerosol source. Viral OTUs from Guliya were traced to metagenomes of the Red Sea and adjacent glaciers on the Tibetan plateau, suggesting both local and regional viral aerosol sources (Zhong *et al.*, 2024). Linkages were made between metagenomes of the Muztagh Ata glacier to ammonia levels and other anthropogenic inputs, with increased prevalence of the gut- and livestock-associated microbiota Nocardiaceae, Muribaculaceae, Lachnospiraceae, and Aerococcaceae, which are proxies for animal husbandry (Liu *et al.*, 2024). Similar inferences on the history of domestic herbivores have been based on detection of the fungus *Sporormiella* as a specific indicator for megafaunal biomass, which has been identified in ice core records from the Italian Alps and Mongolian Altai (Brugger *et al.*, 2018; Festi *et al.*, 2015).

Anthropogenic inputs of black carbon (BC) have been shown to have an interesting relationship with microbes co-registered in ice core records. BC is a combustion byproduct of waste, fossil fuel, and wildfire burning, and is distributed in the atmosphere as a fine, easily aerosolized particulate that is readily deposited in glacial ice. Glacier ice cores have provided critical records of anthropogenic inputs for BC from the last hundred years of industrialization. Bacterial abundance in the glaciers of Tibet has dramatically increased since the early 1990s, concomitant with an increase in dissolved carbon dioxide and levels of BC (Liu *et al.*, 2016). This trend was also observed in the WAIS Divide core, where cell density and BC content increased steadily over the last 70 years (Santibáñez *et al.*, 2018). Analysis of Noijinkangsang and Zuoqiupu showed a gradual increase in BC concentrations from 1980 to 2010, which positively correlated with an increase in total cell counts (Mao *et al.*, 2022).

Interestingly, incidence of low nucleic acid (LNA) and high nucleic acid (HNA) microbial functional groups can be easily screened via flow cytometry and correlated to BC content, and accordingly monsoons. Generally, HNA microorganisms are associated with high nutrient availability and metabolic activity, while LNA are dominant

in oligotrophic conditions. BC in Tibet is deposited by Westerlies during dry periods, which is period where deposition of HNA genera, such as *Actinobacteria,* was highest. Marine microorganisms, generally of the LNA class, predominate in ice core samples from monsoon seasons. How BC increases bacterial abundance when accumulating on glaciers remains unclear, given that it is considered chemically inert and that small particulate size limits its co-incorporation into aerosols with other particles. Work in marine environments suggests that BC may induce biologic hotspots after deposition by absorption of organic carbon and seeding of microbial aggregates (Cattaneo *et al.*, 2010; Malits *et al.*, 2015; Mari *et al.*, 2014). BC was also found to convey protection by absorbing bacteriophages (Cattaneo *et al.*, 2010; Malits *et al.*, 2015).

For those who have studied microbial assemblages in ice cores for decades, learning how to use the data in ways that allow us to link to past atmospheric and climatic conditions remains the Holy Grail. While overarching statements can be made about microbial activity during major climatic phenomenon, such as increases of bacterial abundance during glacial maxima or pre- and post-monsoon seasons, we are only beginning to learn how these glacial biomarkers can be interpreted to appreciate the full story they can tell. The roles and historical abundance of biological aerosols that effect meteorological processes can also be investigated through ice core studies. For instance, data from a ~600-year-old ice core from Greenland shows that INPs varied by more than an order of magnitude, correlated to particle concentrations, and displayed clear annual patterns that implied a source from dust in Greenland and East Asia (Schrod *et al.*, 2020). Most studies have focused on understanding how the atmosphere may have influenced community structures, which has established regional and global trends that are important to understand for the future. Recent advances in low-biomass metagenomics and DNA sequencing have improved our ability to investigate taxonomy of the living and dead material preserved, and provide data to relate ancient metabolic pathways and genes to past conditions. When combined with standard proxies for temperature and atmospheric dust, these tools can allow us to reveal a more detailed picture of past atmospheres and aerobiota than has ever been possible.

⏩ Outlook

Given the logistic challenges associated with studying atmospheric processes, there are explicit advantages in using snow and glacial ice records to learn about the spatial and temporal distributions of bioaerosols in the atmosphere. A pragmatic approach for predicting the environmental consequences of the climate changes currently underway is to better understand the responses of ecosystems and the Earth-atmosphere system to past variability. Various paleoecological records have contributed to what we know about past climates and ecosystems, but none preserve microbes and other biological particles that were distributed in the atmosphere as well as glacial ice. The natural preservation capacity of glaciers provides rare opportunities for studies of past atmospheres and biological conditions that are not possible with other paleorecords.

In terms of the biological ice core data that reveal how past climates affected ancient landscapes, studies of entrapped pollen have been of the most value to date. While ice core palynological records provide important information for understanding past vegetation, ecosystems, and anthropic influence, pollen is a fraction of the biological material that can be interpreted. In particular, the microbes and biogenic material that

are also preserved in glacial ice hold vital clues to environmental and atmospheric conditions from the past. Research on microbes recovered from ancient glacial ice cores has been informative for identifying the range of taxa successful at surviving atmospheric transport and deposition in glacial ice. However, due to the uncertainties associated with linking microbial species or assemblages to specific properties that relate to climatic or atmospheric conditions, use of these data to make interpretations analogous to those possible in palynological studies has been limited. The outlook on this problem is optimistic as recent advances in molecular biology make it possible to characterize the genomic features of all DNA-containing material preserved in the ice. As such, the decades that follow should prove to be an interesting time for discovery.

Knowledge from decades of research coupled with the latest technological innovations have placed researchers in a position to obtain biological and genetic data from ice core materials in ways that were once not possible. However, the outlook for the world's glaciers is less optimistic. There has been extensive retreat of glaciers globally, and based on nearly every prediction, it is virtually certain that accelerated ice loss and thinning will continue across all glaciated regions over the next century. The situation is particularly pressing for alpine glaciers at lower latitudes, which are located near most of the world's population and where continued melting will have profound socioeconomic consequences. If the trends of accelerated melting and reduction in surface area of glaciers are sustained, many smaller glaciers will be lost within our lifetimes, and as they disappear worldwide, so too will the valuable paleo-climatic and -ecological records they have faithfully registered through time.

⏩ Literature cited

Abyzov S.S., *et al*., 1998. Antarctic ice sheet as a model in search of life on other planets. *Adv. Space Res.,* 22 (3), 363-368. https://doi.org/10.1016/S0273-1177(98)00194-X

Achberger A.M., 2011. Expression and partial characterization of an ice binding protein from a bacterium isolated at a depth of 3,519 meters in the Vostok ice core, Antarctica. *Front. Microbiol.*, 2, 255. https://doi.org/10.3389/fmicb.2011.00255

Ahn J., *et al*., 2004. A record of atmospheric CO_2 during the last 40,000 years from the Siple Dome, Antarctica ice core. *J. Geophys. Res.: Atmospheres*, 109 (D13). https://doi.org/10.1029/2003JD004415

Aho K.A., *et al*., 2020. Spatiotemporal patterns of microbial composition and diversity in precipitation. *Ecological Monographs*, 90 (1), e01394. https://doi.org/10.1002/ecm.1394

Allen D., *et al*., 2021. Temporal archive of atmospheric microplastic deposition presented in ombrotrophic peat. *Environ. Sci. Technol. Letters*, 8 (11), 954-960. https://doi.org/10.1021/acs.estlett.1c00697

Alsved M., *et al*., 2020. Natural sources and experimental generation of bioaerosols: Challenges and perspectives. *Aerosol Sci. Technol.*, 54 (5), 547-571. https://doi.org/10.1080/02786826.2019.1682509

Amaretti A., *et al*., 2010. Single cell oils of the cold-adapted oleaginous yeast *Rhodotorula glacialis* DBVPG 4785. *Microbial Cell Factories*, 9 (1), 73. https://doi.org/10.1186/1475-2859-9-73

Amato P., *et al*., 2007. Microorganisms isolated from the water phase of tropospheric clouds at the Puy de Dôme: Major groups and growth abilities at low temperatures: Microorganisms from the water phase of tropospheric clouds. *FEMS Microbiol. Ecol.*, 59 (2), 242-254. https://doi.org/10.1111/j.1574-6941.2006.00199.x

Aubert D., *et al*., 2006. Origin and fluxes of atmospheric REE entering an ombrotrophic peat bog in Black Forest (SW Germany): Evidence from snow, lichens and mosses. *Geochimica et Cosmochimica Acta*, 70 (11), 2815-2826. https://doi.org/10.1016/j.gca.2006.02.020

Bazin L., *et al*., 2013. An optimized multi-proxy, multi-site Antarctic ice and gas orbital chronology (AICC2012): 120–800 ka. *Climate of the Past*, 9 (4), 1715-1731. https://doi.org/10.5194/cp-9-1715-2013

Bidle K.D., *et al*., 2007. Fossil genes and microbes in the oldest ice on Earth. *Proc. Natl Acad. Sci. USA,* 104 (33), 13455-13460. https://doi.org/10.1073/pnas.0702196104

Brugger S.O., *et al*., 2018. Ice records provide new insights into climatic vulnerability of Central Asian forest and steppe communities. *Global and Planetary Change*, 169, 188-201. https://doi.org/10.1016/j.gloplacha.2018.07.010

Bryan N.C., *et al*., 2019. Abundance and survival of microbial aerosols in the troposphere and stratosphere. *ISME J.*, 13 (11), 2789-2799. https://doi.org/10.1038/s41396-019-0474-0

Buford Price P., 2010. Microbial life in martian ice: A biotic origin of methane on Mars? *Planetary and Space Science*, 58 (10), 1199-1206. https://doi.org/10.1016/j.pss.2010.04.013

Bulski K., 2020. Bioaerosols at plants processing materials of plant origin—a review. *Environ. Sci. Pollut. Res. Int.*, 27 (22), 27507-27514. https://doi.org/10.1007/s11356-020-09121-4

Campen R.K., *et al*., 2003. Evidence of microbial consortia metabolizing within a low-latitude mountain glacier. *Geology*, 31 (3), 231-234. https://doi.org/10.1130/0091-7613(2003)031<0231:EOMCMW>2.0.CO;2

Castello J.D., *et al*., 1999. Detection of tomato mosaic tobamovirus RNA in ancient glacial ice. *Polar Biology*, 22 (3), 207-212. https://doi.org/10.1007/s003000050411

Cattaneo R., *et al*., 2010. Association of marine viral and bacterial communities with reference black carbon particles under experimental conditions: An analysis with scanning electron, epifluorescence and confocal laser scanning microscopy. *FEMS Microbiol. Ecol.*, 74 (2), 382-396. https://doi.org/10.1111/j.1574-6941.2010.00953.x

Chen Y., *et al*., 2014. Influence of aeolian activities on the distribution of microbial abundance in glacier ice. *Biogeosciences Discussions*, 11 (10), 14531-14549. https://doi.org/10.5194/bgd-11-14531-2014

Chen Y., *et al*., 2016. Changes of the bacterial abundance and communities in shallow ice cores from Dunde and Muztagata Glaciers, Western China. *Front. Microbiol.*, 7. https://doi.org/10.3389/fmicb.2016.01716

Christner B.C., *et al*., 2000. Recovery and identification of viable bacteria immured in glacial ice. *Icarus*, 144 (2), 479-485. https://doi.org/10.1006/icar.1999.6288

Christner B.C., *et al*., 2008a. Geographic, seasonal, and precipitation chemistry influence on the abundance and activity of biological ice nucleators in rain and snow. *Proc. Natl Acad. Sci. USA,* 105 (48), 18854-18859. https://doi.org/10.1073/pnas.0809816105

Christner B.C., *et al*., 2008b. Ubiquity of biological ice nucleators in snowfall. *Science*, 319 (5867), 1214-1214. https://doi.org/10.1126/science.1149757

Chung A., *et al*., 2024. Age, thinning and spatial origin of the Beyond EPICA ice from a 2.5D ice flow model. *Preprint egusphere*, 2024-1650. https://doi.org/10.5194/egusphere-2024-1650-supplement

de Menezes G.C.A., *et al*., 2020. Fungi in glacial ice of Antarctica: Diversity, distribution and bioprospecting of bioactive compounds. *Extremophiles*, 24 (3), 367-376. https://doi.org/10.1007/s00792-020-01161-5

DeMott P.J., Prenni A.J., 2010. New directions: Need for defining the numbers and sources of biological aerosols acting as ice nuclei. *Atmos. Environ.*, 44 (15), 1944-1945. https://doi.org/10.1016/j.atmosenv.2010.02.032

Duo Saito R.A., *et al*., 2018. Metabarcoding analysis of the fungal biodiversity associated with Castaño Overa Glacier – Mount Tronador, Patagonia, Argentina. *Fungal Ecology*, 36, 8-16. https://doi.org/10.1016/j.funeco.2018.07.006

Failor K.C., *et al*., 2017. Ice nucleation active bacteria in precipitation are genetically diverse and nucleate ice by employing different mechanisms. *ISME J.*, 11 (12), 2740-2753. https://doi.org/10.1038/ismej.2017.124

Festi D., *et al*., 2015. A novel pollen-based method to detect seasonality in ice cores: A case study from the Ortles glacier, South Tyrol, Italy. *Journal of Glaciology*, 61 (229), 815-824. https://doi.org/10.3189/2015JoG14J236

Fracasso I., *et al*., 2024. Exploring different methodological approaches to unlock paleobiodiversity in peat profiles using ancient DNA, *Sci. Tot. Environ.*, 908, 168159. https://doi.org/10.1016/j.scitotenv.2023.168159

Frindte K., *et al.*, 2020. Evidence for signatures of ancient microbial life in paleosols. *Sci. Rep.*, 10 (1), 16830. https://doi.org/10.1038/s41598-020-73938-9

Hoose C., *et al.*, 2010. How important is biological ice nucleation in clouds on a global scale? *Environ. Res. Lett.*, 5 (2), 024009. https://doi.org/10.1088/1748-9326/5/2/024009

Jayaweera K., Flanagan P., 1982. Investigations on biogenic ice nuclei in the Arctic atmosphere. *Geophys. Res. Lett.*, 9 (1), 94-97. https://doi.org/10.1029/GL009i001p00094

Jouzel J., 2013. A brief history of ice core science over the last 50 yr. *Climate of the Past*, 9 (6), 2525-2547. https://doi.org/10.5194/cp-9-2525-2013

Joyce R.E., *et al.*, 2019. Biological ice-nucleating particles deposited year-round in subtropical precipitation. *Appl. Environ. Microbiol.*, 85 (23), e01567-19. https://doi.org/10.1128/AEM.01567-19

Junge K., *et al.*, 2011. Diversity of psychrophilic bacteria from sea ice and glacial ice communities. *In:* Horikoshi K. (éd.), *Extremophiles handbook*, Tokyo, Springer Japan, 793-815. https://doi.org/10.1007/978-4-431-53898-1_39

Knopf D.A., *et al.*, 2011. Stimulation of ice nucleation by marine diatoms. *Nature Geoscience*, 4 (2), 88-90. https://doi.org/10.1038/ngeo1037

Knowlton C., *et al.*, 2013. Microbial analyses of ancient ice core sections from Greenland and Antarctica. *Biology*, 2 (1), 206-232. https://doi.org/10.3390/biology2010206

Králová S., 2017. Role of fatty acids in cold adaptation of Antarctic psychrophilic *Flavobacterium* spp. *Syst. Appl. Microbiol.*, 40 (6), 329-333. https://doi.org/10.1016/j.syapm.2017.06.001

Kumar P., *et al.*, 2024. Bioaerosols downwind from animal feeding operations: A comprehensive review. *J. Hazard. Mater.*, 480, 135825. https://doi.org/10.1016/j.jhazmat.2024.135825

Kyrö E.-M., *et al.*, (2009) Snow scavenging of ultrafine particles: field measurements and parameterization. *Boreal Env. Res.*, 14, 527–538.

Lauer T., *et al.*, 2017. The Agh Band loess-palaeosol sequence – A terrestrial archive for climatic shifts during the last and penultimate glacial–interglacial cycles in a semiarid region in northern Iran. *Quaternary International*, 429, 13-30. https://doi.org/10.1016/j.quaint.2016.01.062

Lindemann J., *et al.*, 1982. Plants as sources of airborne bacteria, including ice nucleation-active bacteria. *Appl. Environ. Microbiol.*, 44 (5), 1059-1063. https://doi.org/10.1128/aem.44.5.1059-1063.1982

Lindow S.E., *et al.*, 1978. Distribution of ice nucleation-active bacteria on plants in nature. *Appl. Environ. Microbiol.*, 36 (6), 831-838. https://doi.org/10.1128/aem.36.6.831-838.1978

Liu Q., *et al.*, 2023. Diversity of the genus *Cryobacterium* and proposal of 19 novel species isolated from glaciers. *Front. Microbiol.*, 14, 1115168. https://doi.org/10.3389/fmicb.2023.1115168

Liu Y., *et al.*, 2016. Bacterial responses to environmental change on the Tibetan Plateau over the past half century. *Environ. Microbiol.*, 18 (6), 1930-1941. https://doi.org/10.1111/1462-2920.13115

Liu Y., *et al.*, 2019. Culturable bacteria isolated from seven high-altitude ice cores on the Tibetan Plateau. *Journal of Glaciology*, 65 (249), 29-38. https://doi.org/10.1017/jog.2018.86

Liu Y., *et al.*, 2020. Genomic insights of cryobacterium isolated from ice core reveal genome dynamics for adaptation in glacier. *Front. Microbiol.*, 11, 1530. https://doi.org/10.3389/fmicb.2020.01530

Liu Y., *et al.*, 2024. Human activity over natural inputs determines the bacterial community in an ice core from the Muztag ata glacier. *Science China Earth Sciences*, 67 (5), 1489-1499. https://doi.org/10.1007/s11430-022-1282-x

López-Moreno J.I., *et al.*, 2024. Marginal snowpacks: The basis for a global definition and existing research needs. *Earth-Science Reviews*, 252, 104751. https://doi.org/10.1016/j.earscirev.2024.104751

Ma L., *et al.*, 1999. Revival and characterization of fungi from ancient polar ice. *Mycologist*, 13 (2), 70-73. https://doi.org/10.1016/S0269-915X(99)80012-3

Madsen P.P., 1981. Peat bog records of atmospheric mercury deposition. *Nature*, 293 (5828), 127-130. https://doi.org/10.1038/293127a0

Maki L.R., *et al.*, 1974. Ice Nucleation Induced by *Pseudomonas syringae*. *Appl. Microbiol.*, 28 (3), 456-459. https://doi.org/10.1128/am.28.3.456-459.1974

Malits A., *et al.*, 2015. Potential impacts of black carbon on the marine microbial community. *Aquatic Microbial Ecology*, 75 (1), 27-42. https://doi.org/10.3354/ame01742

Mao G., *et al*., 2022. Variation of high and low nucleic acid-content bacteria in Tibetan ice cores and their relationship to black carbon. *Front. Microbiol.*, 13, 844432. https://doi.org/10.3389/fmicb.2022.844432

Mari X., *et al*., 2014. Effects of soot deposition on particle dynamics and microbial processes in marine surface waters. *Global Biogeochemical Cycles*, 28 (7), 662-678. https://doi.org/10.1002/2014GB004878

Mayewski P.A., *et al*., 1994. Record drilling depth struck in Greenland. *Eos, Transactions American Geophysical Union*, 75 (10), 113-124. https://doi.org/10.1029/94EO00814

Meola M., *et al*., 2015. Bacterial composition and survival on Sahara dust particles transported to the European Alps. *Front. Microbiol.*, 6, 1454. https://doi.org/10.3389/fmicb.2015.01454

Miteva V., 2008. Bacteria in snow and glacier ice. *In:* Margesin R., *et al*. (eds), *Psychrophiles: From biodiversity to biotechnology*, Berlin, Heidelberg, Springer, 31-50. https://doi.org/10.1007/978-3-540-74335-4_3

Miteva V., *et al*., 2009. Comparison of the microbial diversity at different depths of the GISP2 Greenland ice core in relationship to deposition climates. *Environ. Microbiol.*, 11 (3), 640-656. https://doi.org/10.1111/j.1462-2920.2008.01835.x

Mohaimin A.Z., *et al*., 2023. A critical review on bioaerosols—dispersal of crop pathogenic microorganisms and their impact on crop yield. *Brazilian Journal of Microbiology*, 55 (1), 587-628. https://doi.org/10.1007/s42770-023-01179-9

Moore R.A., *et al*., 2020. Scavenging of sub-micron to micron-sized microbial aerosols during simulated rainfall. *Atmosphere*, 11 (1), 80. https://doi.org/10.3390/atmos11010080

Morris C., Kinkel L., 2002. Fifty years of phyllosphere microbiology: Significant contributions to research in related fields. *Phyllosphere Microbiology*, 365-375.

Morris C.E., *et al*., 2008. The life history of the plant pathogen *Pseudomonas syringae* is linked to the water cycle. *ISME J.*, 2 (3), 321-334. https://doi.org/10.1038/ismej.2007.113

Muhs D.R., *et al*., 2014. Loess records. *In:* Knippertz P., Stuut J.-B.W. (eds), *Mineral dust: A key player in the Earth System*, Dordrecht, Springer Netherlands, 411-441. https://doi.org/10.1007/978-94-017-8978-3_16

Paramonov M., *et al*., 2011. Below-cloud scavenging of aerosol particles by snow at an urban site in Finland. *Boreal Environment Research*, 16 (4), 304-320.

Perini L., *et al*., 2019a. Darkening of the Greenland ice sheet: Fungal abundance and diversity are associated with algal bloom. *Front. Microbiol.*, 10, 557. https://doi.org/10.3389/fmicb.2019.00557

Perini L., *et al*., 2019b. Fungal and bacterial diversity of Svalbard subglacial ice. *Sci. Rep.*, 9 (1), 20230. https://doi.org/10.1038/s41598-019-56290-5

Perini L., *et al*., 2021. Greenland and Svalbard glaciers host unknown basidiomycetes: The yeast *Camptobasidium arcticum* sp. nov. and the dimorphic *Psychromyces glacialis* gen. and sp. nov. *Int. J. Syst. Evol. Microbiol.*, 71 (2), 004655. https://doi.org/10.1099/ijsem.0.004655

Peterson J.M., *et al*., 2024. Ice cores from the Allan Hills, Antarctica show relatively stable atmospheric CO_2 and CH_4 levels over the last 3 million years. *Research Square*, rs.3.rs-5610566/v1. https://doi.org/10.21203/rs.3.rs-5610566/v1

Petit J.R., *et al*., 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, 399 (6735), 429-436. https://doi.org/10.1038/20859

Phillips V.T.J., *et al*., 2009. Potential impacts from biological aerosols on ensembles of continental clouds simulated numerically. *Biogeosciences*, 6 (6), 987-1014. https://doi.org/10.5194/bg-6-987-2009

Phillips V.T.J., *et al*., 2013. Improvements to an empirical parameterization of heterogeneous ice nucleation and its comparison with observations. *J. Atmos. Sci.*, 70 (2), 378-409. https://doi.org/10.1175/JAS-D-12-080.1

Popp T.J., *et al*., 2014. Drilling into debris-rich basal ice at the bottom of the NEEM (Greenland) borehole. *Annals of Glaciology*, 55 (68), 199-206. https://doi.org/10.3189/2014AoG68A029

Price P.B., 2000. A habitat for psychrophiles in deep Antarctic ice. *Proc. Natl Acad. Sci. USA*, 97 (3), 1247-1251. https://doi.org/10.1073/pnas.97.3.1247

Price P.B., 2007. Microbial life in glacial ice and implications for a cold origin of life. *FEMS Microbiol. Ecol.*, 59 (2), 217-231. https://doi.org/10.1111/j.1574-6941.2006.00234.x

Price P.B., *et al.*, 2009. Fluxes of microbes, organic aerosols, dust, sea-salt Na ions, non-sea-salt Ca ions, and methanesulfonate onto Greenland and Antarctic ice. *Biogeosciences*, 6 (3), 479-486. https://doi.org/10.5194/bg-6-479-2009

Pruppacher H.R., Klett J.D., 2010. *Microphysics of clouds and precipitation*, Dordrecht, New York, Springer, 954 p. https://doi.org/10.1007/978-0-306-48100-0

Pummer B.G., *et al.*, 2012. Suspendable macromolecules are responsible for ice nucleation activity of birch and conifer pollen. *Atmos. Chem. Phys.*, 12 (5), 2541-2550. https://doi.org/10.5194/acp-12-2541-2012

Rauch S., *et al.*, 2004. Source characterisation of atmospheric platinum group element deposition into an ombrotrophic peat bog. *Journal of Environmental Monitoring*, 6 (4), 335-343. https://doi.org/10.1039/b316547g

Sánchez-Monedero M.A., *et al.*, 2008. Effect of the aeration system on the levels of airborne micro-organisms generated at wastewater treatment plants. *Water Res.*, 42 (14), 3739-3744. https://doi.org/10.1016/j.watres.2008.06.028

Sands D., *et al.*, 1982. The association between bacteria and rain and possible resultant meteorological implications. *Idojaras*, 86, 148-152 (2-4).

Santibáñez P.A., *et al.*, 2018. Prokaryotes in the WAIS Divide ice core reflect source and transport changes between Last Glacial Maximum and the early Holocene. *Global Change Biology*, 24 (5), 2182-2197. https://doi.org/10.1111/gcb.14042

Schnell R.C., Vali G., 1975. Freezing nuclei in marine waters. *Tellus*, 27 (3), 321-323. https://doi.org/10.1111/j.2153-3490.1975.tb01682.x

Schrod J., *et al.*, 2020. Ice-nucleating particle concentrations of the past: Insights from a 600-year-old Greenland ice core. *Atmos. Chem. Phys.*, 20 (21), 12459-12482. https://doi.org/10.5194/acp-20-12459-2020

Shen L., *et al.*, 2018. Variation with depth of the abundance, diversity and pigmentation of culturable bacteria in a deep ice core from the Yuzhufeng Glacier, Tibetan Plateau. *Extremophiles*, 22 (1), 29-38. https://doi.org/10.1007/s00792-017-0973-8

Shotyk W., *et al.*, 2016. Dust is the dominant source of "heavy metals" to peat moss (*Sphagnum fuscum*) in the bogs of the Athabasca Bituminous Sands region of northern Alberta. *Environ. Int.*, 92-93, 494-506. https://doi.org/10.1016/j.envint.2016.03.018

Singh P., *et al.*, 2013. Taxonomic characterization, adaptation strategies and biotechnological potential of cryophilic yeasts from ice cores of Midre Lovénbreen glacier, Svalbard, Arctic. *Cryobiology*, 66 (2), 167-175. https://doi.org/10.1016/j.cryobiol.2013.01.002

Stewart C., Fergusson J.E., 1994. The use of peat in the historical monitoring of trace metals in the atmosphere. *Environmental Pollution*, 86 (3), 243-249. https://doi.org/10.1016/0269-7491(94)90164-3

Szyrmer W., Zawadzki I., 1997. Biogenic and anthropogenic sources of ice-forming nuclei: A Review. *Bull. Am. Meteorol. Soc.*, 78 (2), 209-228. https://doi.org/10.1175/1520-0477(1997)078<0209:BAASOI>2.0.CO;2

Thompson L.G., *et al.*, 1997. Tropical climate instability: The last glacial cycle from a Qinghai-Tibetan ice core. *Science*, 276 (5320), 1821-1825. https://doi.org/10.1126/science.276.5320.1821

Thompson L.G., *et al.*, 2002. Kilimanjaro ice core records: Evidence of Holocene climate change in tropical Africa. *Science*, 298 (5593), 589-593. https://doi.org/10.1126/science.1073198

Thompson L.G., 2017. Past, present, and future of glacier archives from the world's highest mountains. *Proc. Am. Philos. Soc.*, 161 (3), 226-243. https://www.jstor.org/stable/45211558

Tobo Y., *et al.*, 2013. Biological aerosol particles as a key determinant of ice nuclei populations in a forest ecosystem. *J. Geophys. Res.: Atmospheres*, 118 (17), 100-110. https://doi.org/10.1002/jgrd.50801

Tsuji M., *et al.*, 2022. Glacier retreat results in loss of fungal diversity. *Sustainability*, 14 (3), 1617. https://doi.org/10.3390/su14031617

Tung H.C., *et al.*, 2005. Microbial origin of excess methane in glacial ice and implications for life on Mars. *Proc. Natl Acad. Sci. USA*, 102 (51), 18292-18296. https://doi.org/10.1073/pnas.0507601102

Tung H.C., *et al.*, 2006. Microorganisms metabolizing on clay grains in 3-km-deep Greenland basal ice. *Astrobiology*, 6 (1), 69-86. https://doi.org/10.1089/ast.2006.6.69

Vali G., 1995. Principles of ice nucleation. *In*: Lee R.E., *et al*., eds. *Biological ice nucleation and its applications*. APS Press, St Paul, Minnesota, 1-28.

Vuille M., *et al*., 2008. Climate change and tropical Andean glaciers: Past, present and future. *Earth-Science Reviews*, 89 (3-4), 79-96. https://doi.org/10.1016/j.earscirev.2008.04.002

Weil T., *et al*., 2017. Legal immigrants: Invasion of alien microbial communities during winter occurring desert dust storms. *Microbiome*, 5 (1), 32. https://doi.org/10.1186/s40168-017-0249-7

Willerslev E., *et al*., 2007. Ancient biomolecules from deep ice cores reveal a forested southern Greenland. *Science*, 317 (5834), 111-114. https://doi.org/10.1126/science.1141758

Wilson T.W., *et al*., 2015. A marine biogenic source of atmospheric ice-nucleating particles. *Nature*, 525 (7568), 234-238. https://doi.org/10.1038/nature14986

Xiang S.R., *et al*., 2004. Bacterial diversity in malan ice core from the Tibetan Plateau. *Folia Microbiologica*, 49 (3), 269-275. https://doi.org/10.1007/BF02931042

Xiang S.R., *et al*., 2009. Deposition and postdeposition mechanisms as possible drivers of microbial population variability in glacier ice. *FEMS Microbiol. Ecol.*, 70 (2), 165-176. https://doi.org/10.1111/j.1574-6941.2009.00759.x

Xie W., *et al*., 2021. The source and transport of bioaerosols in the air: A review. *Front. Environ. Sci. Engineering*, 15 (3), 44. https://doi.org/10.1007/s11783-020-1336-8

Yao T., *et al*., 2006. Microorganisms in the Malan ice core and their relation to climatic and environmental changes. *Global Biogeochemical Cycles*, 20 (1). https://doi.org/10.1029/2004GB002424

Yao T., *et al*., 2008. Bacteria variabilities in a Tibetan ice core and their relations with climate change. *Global Biogeochemical Cycles*, 22 (4). https://doi.org/10.1029/2007GB003140

Zhang L., *et al*., 2013. Review and uncertainty assessment of size-resolved scavenging coefficient formulations for below-cloud snow scavenging of atmospheric aerosols. *Atmos. Chem. Phys.*, 13 (19), 10005-10025. https://doi.org/10.5194/acp-13-10005-2013

Zhang S., *et al*., 2007. Culturable bacteria in Himalayan glacial ice in response to atmospheric circulation. *Biogeosciences*, 4 (1), 1-9. https://doi.org/10.5194/bg-4-1-2007

Zhong Z.-P., *et al*., 2021. Glacier ice archives nearly 15,000-year-old microbes and phages. *Microbiome*, 9 (1), 160. https://doi.org/10.1186/s40168-021-01106-w

Zhong Z.-P., *et al*., 2024. Glacier-preserved Tibetan Plateau viral community probably linked to warm–cold climate variations. *Nature Geoscience*, 17 (9), 912-919. https://doi.org/10.1038/s41561-024-01508-z

Section 3

The extent of aerial voyages and their impact on disease epidemiology and environmental quality

Chapter 11

An overview of the demographic and genetic toolbox for assessing wind-assisted dispersal

Margaux Darnis, Karine Berthier

Long-distance dispersal (LDD) is critical for maintaining metapopulation dynamics and colonizing new habitats (Hanski, 2001; Nathan, 2013). As such, it is a key process in predicting risks to plants, animals and humans, arising from the introduction of new taxa of pathogens and insect vectors or pests. It also includes the recurrent dispersal of such organisms under source-sink dynamics, i.e. a population can persist in sink habitats only through continuous immigration from source habitats, potentially disrupting local pest management or eradication efforts (Kim and Sappington, 2013; Liebhold and Tobin, 2008; Mundt *et al.*, 2009). For instance, Huestis *et al.* (2019) used helium balloons to sample airborne insects and found that air currents enable malaria vectors to migrate frequently over hundreds of kilometers, thus contributing to the persistence of the disease in areas where it had nearly been eradicated or where long-term survival would be impossible due to unfavorable environmental conditions. Similarly, in Japan, evidence suggests that the Oriental fruit fly *Bactrocera dorsalis*, which was believed to have been eradicated in the 1980s but continues to be captured in trap surveillance networks, can periodically recolonize the island through wind-assisted dispersal from native areas located hundreds of kilometers away (Otuka *et al.*, 2019). Human-assisted LDD has been well documented for many taxa, with key examples such as the transport of *Aedes albopictus* via the shipment of used tires infested with mosquito eggs or air travel (Deblauwe *et al.*, 2022; Rezza, 2014; Tatem *et al.*, 2012). In contrast, despite its importance, aerial LDD and its consequences for the spatial distribution of pathogens and their vectors as well as pest insect species (see Kim and Sappington (2013) for a review on the boll weevil) are often overlooked in surveillance strategies (Atieli *et al.*, 2023; Gao *et al.*, 2016; Huestis *et al.*, 2019; Morris *et al.*, 2021).

Dispersal is a multifaceted word. A dispersal event can be divided into three phases: 1) the emigration phase, during which an organism leaves its habitat/host, 2) the transfer phase, where the organism moves through the environment, and 3) the immigration phase, during which the organism establishes itself in a new habitat or a new host (Pflüger and Balkenhol, 2014). Each of these phases is under different constraints (Cayuela *et al.*, 2018). First, the flow of individuals between sites depends on the fraction of the local source population that leave its original habitat (i.e., emigration rate). In the case of wind-assisted dispersal, this depends on the ability of individuals to be

passively or actively loaded into the air mass. The transfer phase, which determines the ability to reach new habitats depends mainly on the environmental conditions (e.g., temperature within the air mass). Finally, the immigration phase determines the ultimate success of dispersal events, requiring favourable conditions for the release of individuals from the air mass and their subsequent establishment in the new habitat (Sturtevant *et al.,* 2013; see also Chapters 9 and 14). Dispersal can be very costly and a large proportion of individuals/propagules may die before reaching new habitats or after landing due to unsuitable environmental conditions or exhaustion. The causes and/or consequences of the dispersal phases have motivated years of research in various fields, including ecology, conservation biology and evolutionary biology (Matthysen, 2012).

Demographic studies generally rely on direct techniques such as marking and recapturing individuals or radio tracking, to estimate dispersal characteristics (e.g., travelled distance, travelling time, path taken) and its demographic consequences (e.g., demographic rescue). However, assessing LDD using demographic approaches such as capture-mark-recapture is challenging for any taxa (Cain *et al.,* 2003), and even more so for very small or nearly invisible organisms with large population sizes and dispersal abilities (Nathan *et al.*, 2003; Jacquet *et al.*, 2016), as it is often the case for insect pest and vector species as well as pathogens (Osborne *et al.,* 2002; Brown and Hovmøller 2002; Asplen, 2018). Alternatively, population genetic methods, based on neutral molecular markers, have been widely used on a variety of taxa as an indirect approach to gain understanding on the dispersal process, including long-distance wind-assisted dispersal (Kim and Sappington, 2013). For example, by combining population genetic analyses with air trajectory simulations, Li *et al.* (2023) found evidence that Chinese populations of the *Puccina striiformiss* strain, responsible for wheat yellow rust, exhibited a source-sink dynamics driven by air currents between the southern wheat production basins, where the pathogen persists year-round, and the northern basins, where the obligate host is absent during the summer. It should be noted, however, that population genetic studies generally do not provide a direct estimate of dispersal, as they focus primarily on analysing genetic diversity sampled from different localities to assess population structure, which is shaped in part by gene flow, i.e. the effective dispersal of individuals that have successfully moved, established, and reproduced in new habitats. When effective dispersal is frequent, populations tend to homogenize genetically, while under limited gene flow, populations are expected to differentiate due to genetic drift effects, i.e. the random fluctuations in the frequency of gene variants in a population, which can lead to the loss of genetic diversity over time, especially in small populations.

This chapter provides a synthetic overview of demographic (defined here as methods based on direct observations of individual, population movements, spatio-temporal variations in occurrence/abundance) and genetic approaches that can be used to test for the occurrence of long-distance wind-assisted dispersal of insects and, to some extent, pathogens. Terminology used in studies of long-distance dispersal can vary significantly across research fields, leading to potential confusion. For instance, studies on insects often refers to long-distance movements as migration, defined as an individual-based behavioral phenomenon, while dispersal is considered as one-way intergenerational movements (see Chapter 9). In ecology, and in this chapter, migration is typically defined as the collective movement of multiple individuals within a

population in a seasonal or multi-annual (i.e. multigenerational) round trip from one location to another, which does not always result in dispersal or gene flow. In contrast, dispersal refers to one-way movements of individuals away from their birthplace to a new location, often in search of resources or a suitable environment where they may establish a new population or integrate into an existing one, thereby contributing to gene flow. Adding to the confusion, in population genetics, the term migration specifically refers to the proportion of genes in a subpopulation that originate from new immigrants at each generation (see Cayuela *et al.* (2018) for detailed definitions). This chapter will provide examples of both types of long-distance movement, with an emphasis on how their differences may influence the interpretation of LDD studies, especially those based on genetic data.

⏩ Estimating the "windscape"

The identification of potential aerial pathways (i.e. potential wind-driven dispersal routes) connecting known populations or areas of interest is essential for assessing and accounting for LDD, especially at large spatial scales. Such knowledge is not only valuable for guiding and optimizing the design of demographic and genetic samplings and to parametrize spread models (Liebhold and Tobin, 2008; Choufany *et al.,* 2021; Bibard *et al.,* 2024a, 2024b) but also for ensuring compliance with regulations regarding the sampling of biological material across different countries, such as the Nagoya Protocol. Today, various methodological developments are facilitating the computation of potential aerial connectivity networks between sites/areas (Gao *et al.*, 2020). For example, the development of Lagrangian based models such as HYSPLIT (Hybrid Single-Particle Lagrangian Integrated Trajectory; Stein *et al.,* 2015) or NAME (Numerical Atmospheric-dispersion Modelling Environment; Jones *et al.,* 2007) now allows reconstructing air-mass movements on a global scale with fine spatio-temporal resolutions (Choufany *et al.*, 2021). Moreover, recent developments of dedicated tools, such as the web application Tropolink[7] (Richard *et al.*, 2023), further facilitate the computation of air-mass trajectories based on the HYSPLIT model as well as the resulting connectivity networks; a task that can be challenging for non-specialists. Based on ecological knowledge of the species under study (e.g., seasonal dynamics, diurnal or nocturnal flight), backward or forward trajectories can be computed from a set of locations over a given duration. Attributes of each trajectory (e.g., hourly positions in longitude, latitude and altitude and various meteorological indices such as temperature or pressure) can be used to select the trajectories to include in the computation of the aerial connectivity between the locations that form the nodes of the network. For example, trajectories with sections of very low temperature that are unrealistic with individual survival in the air mass can be filtered out before computing connectivity networks (see Chapter 14 for examples and Chapter 4 for information on the estimation of air mass trajectories and aerial connectivity networks and uses of transport models). Modelling of air mass trajectories has been used to approximate LDD of various insect species, such as the boll weevil (*Anthomnus grandis*), fall armyworm (*Spodoptera frugiperda*), sugarcane aphid (*Melanaphis sacchari*), moths *(Cornifrons ulceratalis)* and *Culicoides*, and are crucial for establishing control measures and forecasting introduction and spread

7. https://tropolink.fr/

of insect pest species or vector-borne diseases (Dantart *et al.,* 2009; Westbrook *et al.,* 2011, 2016; Burgin *et al.,* 2013; Eagles *et al.,* 2014; Schmale and Ross, 2015; Koralewski *et al.,* 2021; Bibard *et al.,* 2024a, 2024b).

Figure 11.1 illustrates how the exploration of the windscape can strengthen hypotheses about aerial dispersal, help optimize sampling design and effort, and anticipate compliance with international regulations. Monthly backward air masses trajectories were computed using the HYSPLIT model for a study on the invasive oriental fruit fly, *Bactrocera dorsalis*, a major pest of mango crops in Senegal. The trajectories were calculated from several orchards located in the Niayes area, the northernmost and latest mango-producing region in West Africa (from June to September). In this region, where environmental conditions are quite unfavorable for *B. dorsalis*, populations exhibit well-marked annual fluctuations in abundance, with a striking demographic bottleneck that leads to the near disappearance of flies during the off-season for mangos. Using 2012-2014 time-series of *B. dorsalis* abundance collected from 65 orchards in the Niayes, Caumette *et al.* (2024) found that local population growth can start as early as March-April (before the mango season), while the latest onset occurred in June-July. One hypothesis for the early seasonal infestation of certain orchards in the Niayes is wind-assisted dispersal from other, more precocious mango-producing areas. The surface air system in Senegal is influenced by the seasonal shift of the Intertropical Convergence Zone, which alternates between the southwest monsoon flow, predominating between June and October, and the northeast continental (harmattan) and north oceanic trade winds. Although southerly winds are rare prior to the onset of the monsoon, computation of backward air mass trajectories from Niayes orchards in March and April of 2012-2014 suggests that coastal southerly winds could be responsible for the early arrival of *B. dorsalis* from early mango production basins in southwestern Senegal and Guinea-Bissau.

⏩ Demographic-based assessment of wind-assisted LDD

Mark-recapture techniques and radio-tracking

Marking (lab or wild) individuals and recapturing them at a range of distances from their release point is a widely used technique to assess insect movements over space and time (Akhter *et al.*, 2023; Hagler and Jackson, 2001; Kim and Sappington, 2013; Osborne *et al.*, 2002; Terui, 2020). When individual identification is possible through marking, this approach provides a direct measure of individual dispersal while mass marking (e.g., spraying non-toxic paint or dye on a large number of individuals) offers insights into movement patterns at the population level. A large range of procedures have been used to mark individuals, including both artificial markers such as inks, tags, stickers, paints, fluorescent substances, rare elements, and natural markers already present on the individuals such as pollen, algae, phoretic mites, pathogens, gut contents, radioactive isotopes or genetic mutations (Gorki *et al.*, 2024; Hagler and Jackson, 2001; Osborne *et al.*, 2002; Reich *et al.*, 2023; Reynolds *et al.*, 2006). Although recapture rate is often low for insects –e.g., 0.02% for *Culicoides* biting midge (Kluiters *et al.*, 2015); 5 to 10% for *Aedes aegypti* (Ross *et al.*, 2017); 0.45 to 3% for *Bactrocera dorsalis* (Chailleux *et al.*, 2021)–, such techniques have been successfully used at the landscape scale to study movements in butterflies (e.g, Baguette, 2003; Zimmermann *et al.,* 2011), for the tobacco budworm

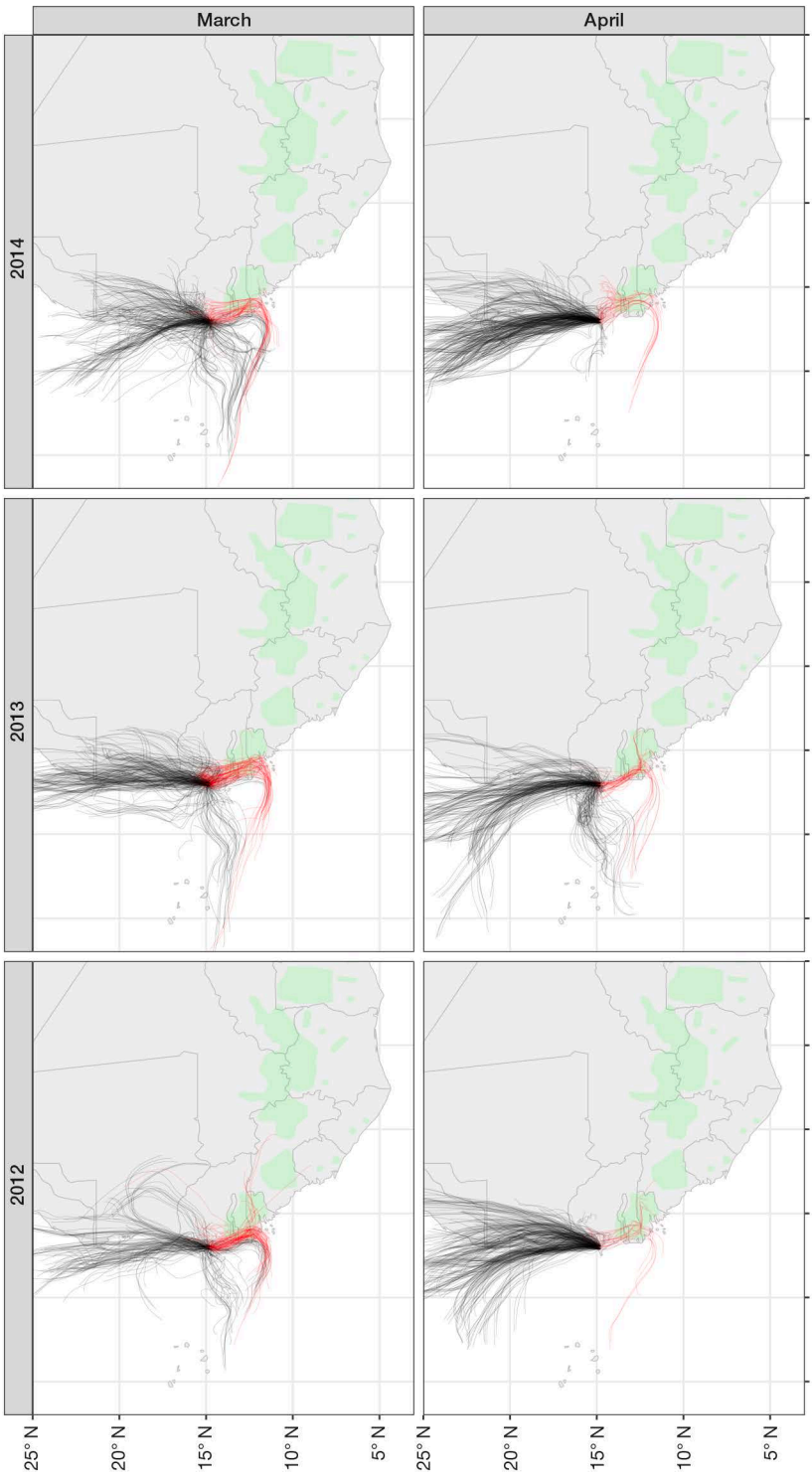

Figure 11.1. Example of monthly backward air masses trajectories computed using the HYSPLIT model for a study on the invasive oriental fruit fly, *Bactrocera dorsalis*, a major pest of mango crops in Senegal.

Trajectories were computed for the period covering March and April in 2012, 2013 and 2014. Backward trajectories crossing over early mango production basins (green patches) at an altitude under 200 meters are indicated in red, otherwise trajectories are shown in black.

Heliothis virescens (Schneider, 1999), the noctuid moth *Agrotis ipsilon* (Showers *et al.*, 1993), the Queensland fruit fly *Bactrocera tryoni* (Meats and Edgerton, 2008), *Culicoides* biting midges (Kluiters *et al.*, 2015), and the medfly *Ceratitis capitata* (Meats and Smallridge, 2007). Mark-recapture-based inference methods clearly play a pivotal role in estimating dispersal parameters. However, they remain challenging because they are highly dependent on the design used to collect the data and subject to various sources of bias in the estimation procedures, such as tag loss, variability in detection, effects of tags on individual movement and survival, and dispersal outside the study area (Lindberg, 2012; Nathan, 2013; Terui, 2020; Badia-Boher *et al.,* 2023). While designs may be relatively simple and cost-effective at small scales, marking-recapture techniques are generally considered inadequate to assess LDD as the sampling effort for recapture (e.g., number and distribution of traps) become unreachable at large scales (Nathan *et al.*, 2003), especially without any assumption on the most probable recipient areas of LDD. In the context of long-distance wind-assisted dispersal, using information on the most likely dispersal sources and recipient areas can provide opportunities to design *ad hoc* capture-mark-recapture studies at large scales to directly assess airborne dispersal. Advances in the miniaturization of radio transmitters have also opened opportunities for radio-tracking movements of insect species (Daniel Kissling *et al.,* 2014). Although radio transmitters weighted almost 50% of the individual body mass, Knight *et al.* (2019) tracked migratory movements of monarch butterflies and common green darner dragonflies over more than 100 km in North America thanks to an automated radio-telemetry network of about 100 towers (i.e. Motus Wildlife Tracking system; Taylor *et al.,* 2017). In absence of such a network, tracking can be achieved from an airplane, as it has been done in the Alps Mountains to determine the degree of wind assistance in the migratory movement of death's-head hawkmoth moths equipped with Very High frequency (VHF) radio-transmitters (Menz *et al.*, 2022).

Aerial sampling and sensors

Various aerial platforms have been used since after World War II to sample insects and microorganisms directly from the atmosphere to get insights on their dispersal patterns (Hollinger *et al.,* 1991; Greenstone *et al.,* 1991; Chapman *et al.,* 2004; Grinshpun *et al.,* 2015; Datsugwai Mohammed and Balogu, 2023). Airplanes and drones equipped with devices to filter the air stream allowed to collect and identify a wide range of bacteria and fungi at various altitudes, further confirming that microorganisms can be dispersed up to thousands of kilometers (Smith *et al.,* 2018; Bryan *et al.,* 2019; Rodó *et al.,* 2024). Insects are generally collected using nets and sticky traps attached to aircraft, helium balloons, kites or drones (Berry and Taylor, 1968; Irwin *et al.,* 1988; Isard *et al.,* 1990; Hollinger *et al.,* 1991; Greenstone *et al.,* 1991; Chapman *et al.,* 2004; Miao *et al.,* 2013; Löcken *et al.,* 2020; Greenslade *et al.,* 2021; Yaro *et al.,* 2022). Such techniques allowed, among others, to assess the diversity, dynamics, direction and magnitude of high-altitude migrating insects in Sahel (Florio *et al.*, 2020), or to describe potential source-sink dynamics of malaria insect vectors in Sahel (Huestis *et al.*, 2019) or wheat midges in China (Miao *et al.*, 2013). More recently, the incorporation of radars has enhanced aerial sampling accuracy by allowing positioning the nets within layers of concentrated migrants (Reynolds *et al.*, 2006; Riley, 1992). Systems such as Vertical Looking Radar (VLR), are also used to

scan the air column for masses of flying insects and produce density-height profiles throughout day and night, as well as information on biomass and insect diversity based on morphological characteristics (Abd El-Ghany *et al.,* 2020; Huang *et al.,* 2024; Bauer *et al.*, 2024). For example, such technology was used to quantify the annual flux of high-flying insects migrating over the United Kingdom to approximately 3.5 trillion of individuals representing 3,200 tons of biomass (Hu *et al.,* 2016). Other radar technologies have been developed, such as harmonic or doppler radar, and new innovations are still emerging, proving the value of radar entomology to decipher insect dispersal (Noskov *et al.,* 2021). Today, advances in spatial, temporal and spectral resolution of remote sensing also provide opportunities to determine, directly or indirectly (i.e. through their effects on the environment like crop stresses, damages or disease development), the abundance and movements of insects (reviewed in Prasad *et al.,* 2012; Bauer *et al.,* 2019; Becciu *et al.,* 2019; Abd El-Ghany *et al.,* 2020; Rhodes *et al.,* 2022). These technologies have been applied to detect dispersing corn leaf aphids and sweet potato whitefly infestations through the presence of sooty mold in the fields (Acharya and Thapa, 2015).

Ground trapping and trap networks

Trapping techniques are widely used to monitor insect occurrence and abundance, to forecast pest outbreak and implement population management strategies at different spatial scales (reviewed in Osborne *et al.,* 2002; Prasad and Prabhakar, 2012). Pheromone traps, which use synthetic chemical molecules mimicking natural pheromones emitted by insects to communicate, are intensively used as they are species-specific and highly attractive, allowing monitoring of low-density populations. This technique has been instrumental in applications such as early detection, monitoring, mating disruption, population control and eradication of various insects (Witzgall *et al.,* 2010; Prasad and Prabhakar, 2012; Alam *et al.,* 2023). Other types of traps exists, such as light traps, which are extensively used to study population dynamics of flying insects attracted to light sources such as many Lepidoptera and Coleoptera species (Bjerge *et al.*, 2021; Dadmal and Khadakkar, 2014; Wolda, 1992), suction traps that capture flying insects by drawing them into a trap using a powerful vacuum and are often positioned at fixed locations and heights to monitor populations over long periods (Luquet *et al.*, 2023; Schoeny and Gognalons, 2020), and coloured sticky traps that attract insect species drawn to certain colours such as yellow sticky traps for aphids (Flores *et al.*, 2009; Schoeny and Gognalons, 2020). Long term trap networks have been deployed to monitor and forecast population dynamics of major pest insects, such as the African armyworm *Spodoptera exempta* in eastern Africa (Rose *et al.,* 2000), moths and aphids –e.g., the Rothamsted insect survey; Harrington and Woiwod (2007), or the EXAMINE (Exploitation of Aphid Monitoring systems IN Europe) project; Harrington (2001); Cocu *et al.* (2005)– or the migration capabilities of psyllids as disease vectors, e.g. *Cacospylla pruni*, vector of *Candidatus* Phytoplasma prunorum (Greenslade *et al.,* 2020*,* 2021). Recently, Gandiaga and James (2023) combined phenological information with time-series of ground captures to estimate long-distance dispersal (assumed to be wind-assisted) of the eastern spruce budworm (*Choristoneura fumiferana*) in Quebec. Based on a previously developed phenological model and Canadian weather data, the authors calculated the daily probability of moth emergence during the flight season for each cell of a raster of 10 km resolution. The modelled confidence intervals

of emergence probability were used to classify collected individuals as either residents or migrants. For the latter, the potential source locations within the study area were identified as the locations in phenological synchrony with the capture event. The fit of dispersal kernels to the distribution of Euclidean distances, computed between the locations of migrant capture events and the nearest points in phenological synchrony, suggested that many individuals dispersed up to 450 km.

⏩ Genetic-based assessment of wind-assisted LDD

Genetic approaches to assessing LDD assume that some level of genetic structure can be observed (Cornuet *et al.*, 1999). Indeed, even when working at relatively large spatial scales, genetic structure may actually be absent or very weak, especially for organisms with very large population sizes, as it is often the case for insect pest species and pathogens. For example, using microsatellite markers, Chapuis *et al.* (2011) showed that the very large population sizes of the Australian plague locust, *Chortoicetes terminifera*, resulted in genetic homogeneity across the whole Australian continent, which precluded straightforward estimation of gene flow between populations located on the western and eastern coasts. The observed genetic homogeneity does not necessarily result from intensive contemporary gene flow, and then does not imply that the different sampling sites are well connected by long-distance dispersal, but rather reflects historical connectivity and shared ancestral polymorphisms. Such a lack of genetic differentiation across large scales is also a common result in marine systems and it has also often been attributed to large effective population sizes that dampen genetic drift effects (Waples *et al.*, 2008). Estimates of genetic differentiation and gene flow depends partly on the number and characteristics of the genetic markers used in the analysis (Chapuis *et al.*, 2011; Gautier *et al.*, 2022; Marko and Hart, 2011). In such situations, advances in the field of molecular biology with the development of genome-wide genetic markers provide new opportunities to detect weak genetic structure and infer movement, compared to more traditional markers such as highly polymorphic microsatellites (Dufresnes *et al.*, 2023; Sunde *et al.*, 2020).

The "Isolation-By" framework

In population genetics, LDD generally refers to movements occurring over long distances but at a very low frequency. Thus, under spatially limited gene flow, distant populations are expected to differentiate under genetic drift effects. In a continuously distributed population, this is referred to as the Isolation-by-Distance (IBD) model, in which individuals disperse their genes according to a decreasing function of spatial distance (Wright, 1943). The most common method to test for IBD is to regress genetic measures of differentiation, computed either at the population level –e.g., F_{ST}; see Rousset (1997)– or the individual level –e.g., a; see Rousset (1999)–, against geographic distances. The original IBD model has been further extended in the field of landscape genetics assuming that in a heterogeneous landscape, dispersal will vary in space according to the permeability of the different landscape features to individual movements (Balkenhol *et al.,* 2009). Accordingly, in the regression model geographic distances between sampled sites can be replaced by landscape distances/paths, based on cost or resistance values to dispersal, which are attributed to landscape features. In the context of wind-assisted LDD, a similar line of reasoning can be applied to aerial

connectivity, with the assumption that sites highly connected by wind trajectories represent predominant dispersal pathways (Kling and Ackerly, 2021). The windscape model and the strict IBD model can then be compared to determine how much of the pattern of genetic structure is best explained by geographic distance (isolation-by-distance: between-sites genetic differentiation increases with geographic distance) or by aerial connectivity (isolation-by-wind: genetic differentiation is higher between sites that are weakly connected by air masses). For example, Leyronas *et al.* (2018) showed that aerial connectivity between distant sites in France was a better indicator than geographic distance to predict the genetic composition of the incoming inoculum of *Sclerotinia sclerotiorum* in a given site. In the field of landscape genetics, Mantel and partial Mantel tests are the most common approach to test the correlation between the pairwise matrices of genetic, geographic and landscape distances (see Diniz-Filho *et al.* (2013) and Guillot and Rousset (2013) for a debate on the use of simple and partial Mantel tests and alternative approaches). Since the IBD process is considered the neutral model of population structure, the rationale for using the partial Mantel test is that it allows disentangling landscape effects on genetic structure from the effects of geographic isolation due to spatially restricted dispersal. This is achieved by computing the correlation between genetic and landscape distances while controlling for geographic distance (see Kling and Ackerly (2021) for an example, including estimates of wind connectivity). A conceptual illustration of the "isolation-by" framework is presented in Figure 11.2, highlighting potential genetic outcomes based on the degree of genetic structure and the characteristics of both long-distance movements (migration or dispersal) and recipient sites of these movements (e.g., breeding or feeding grounds; unoccupied or already inhabited sites).

It is worth noting that when using metrics of genetic differentiation, such as F_{ST}, once should keep in mind that they are not a measure of gene flow, or dispersal, but rather reflect interactions between evolutionary forces, including genetic drift, gene flow and mutation along the demographic history of the populations (Marko and Hart, 2011; Richardson *et al.*, 2016; Whitlock and Mccauley, 1999). Relationships between gene flow and F_{ST} measures have mostly been formalized under the theoretical island model (where $F_{ST} = 1/(4Nm+1)$, with Nm = effective population size × migration rate) and the isolation-by-distance model (where the slope of the regression of $F_{ST}/(1-F_{ST})$ as a function of the logarithm of geographic distance provides an estimate of Do^2, the product of effective population density and average squared axial parent–offspring distance). Both models rely on assumptions that are unlikely to be met in the context of wind-assisted dispersal, such as constant migration and population size for the former and spatial and temporal homogeneity of the density and dispersal parameters for the latter. Accurate inference of gene flow remains a challenging task in population genetics, relying on the development of efficient statistical methods to test underlying demographic models and detect admixture (Adams *et al.,* 2019). Nevertheless, estimates of F_{ST} are still very valuable and relatively easy to compute to describe population structure and gain insight on population connectivity, but they should be interpreted carefully in terms of gene flow and in the light of additional information on current and historical demography (Holsinger and Weir, 2009). Estimates of genetic differentiation or gene flow also generally reflect processes in both directions (e.g., symmetrical gene flow between sampled locations), while wind currents and subsequent dispersal may be highly asymmetric (Gillespie *et al.*, 2012). Methods, such

as *divMigrate* (Sundqvist *et al.*, 2016), that allow directional genetic differentiation and gene flow, may be more appropriate when assessing wind-assisted dispersal (see Kling and Ackerly (2021) for an example) Finally, testing the "isolation-by" hypothesis to assess aerial dispersal may require important sampling effort at relatively large scales to adequately represent the distribution of between-site geographic distance and wind connectivity (Wang and Bradburd, 2014).

The "Source" framework

Under this framework, the goal is to assign individuals sampled in the potential recipient areas of LDD to their putative populations of origin. Genetic assignment methods are then a more appropriate approach to estimate current gene flow by identifying immigrants in a sampled population and, determining their most likely sources (Paetkau *et al.*, 2004). Genetic delineation of the putative populations of origin is often based on the results of clustering analyses in which the number of these potential sources (*K*) can be determined using distance-based methods, such as k-means and hierarchical clustering (e.g., Discriminant Analysis on Principal Components such as implemented in the R package '*adegenet*'; Jombart, 2008; Jombart *et al.,* 2010; Jombart and Ahmed 2011), or with model-based methods assuming within-group Hardy-Weinberg and linkage equilibrium such as Bayesian or maximum-likelihood methods including STRUCTURE (Pritchard *et al.*, 2000; Raj *et al.*, 2014) and ADMIXTURE (Alexander *et al.,* 2009). In model-based methods, inference of admixture proportions allows estimation of the part of the individuals genome derived from each identified genetic cluster (ancestry coefficients), and then to assign each individual to one genetic source with a given level of confidence. A conceptual illustration of this framework is presented in Figure 11.2, with the proportion of individual genomes sampled from the recipient area being assigned to putative source populations (i.e. the genetic clusters identified). The number of individuals assigned to different sources can be determined using a threshold based on the proportion of an individual's genome assigned to each genetic cluster (e.g., 80%). These numbers can then serve as a measure of genetic connectivity, which is expected to positively correlate with highest probabilities of aerial connectivity in cases of wind-assisted dispersal. The power and accuracy of the genetic assignment methods will however depend on the number of individuals sampled, the specificities of the genetic markers, the number of loci, and the level of structuration between the *K* populations identified. On this last point, the partitioning into *K* populations resulting from the clustering analyses, and then the accuracy of individual assignments, can be strongly influenced by the sampling scheme, e.g. realistic sampling of immigrant population sources, accurate spatial coverage at the spatial scale considered and coherent with the current and/or past demographic history of populations (Lawson *et al.,* 2018).

This "source" framework was applied to evaluate the source-sink dynamics attributed to recurrent LDD by monsoon winds in the brown planthopper, *Nilaparvata lugens*, a major pest of rice crops that reproduces year-round in the tropical parts of its distribution and, seasonally, recolonizes Asian temperate areas where the species cannot overwinter (Hereward *et al.,* 2020; Hu *et al.,* 2024). Using principal component analysis (PCA) and admixture analyses to define the main putative source populations to which samples from the non-overwintering sites were assigned, these studies

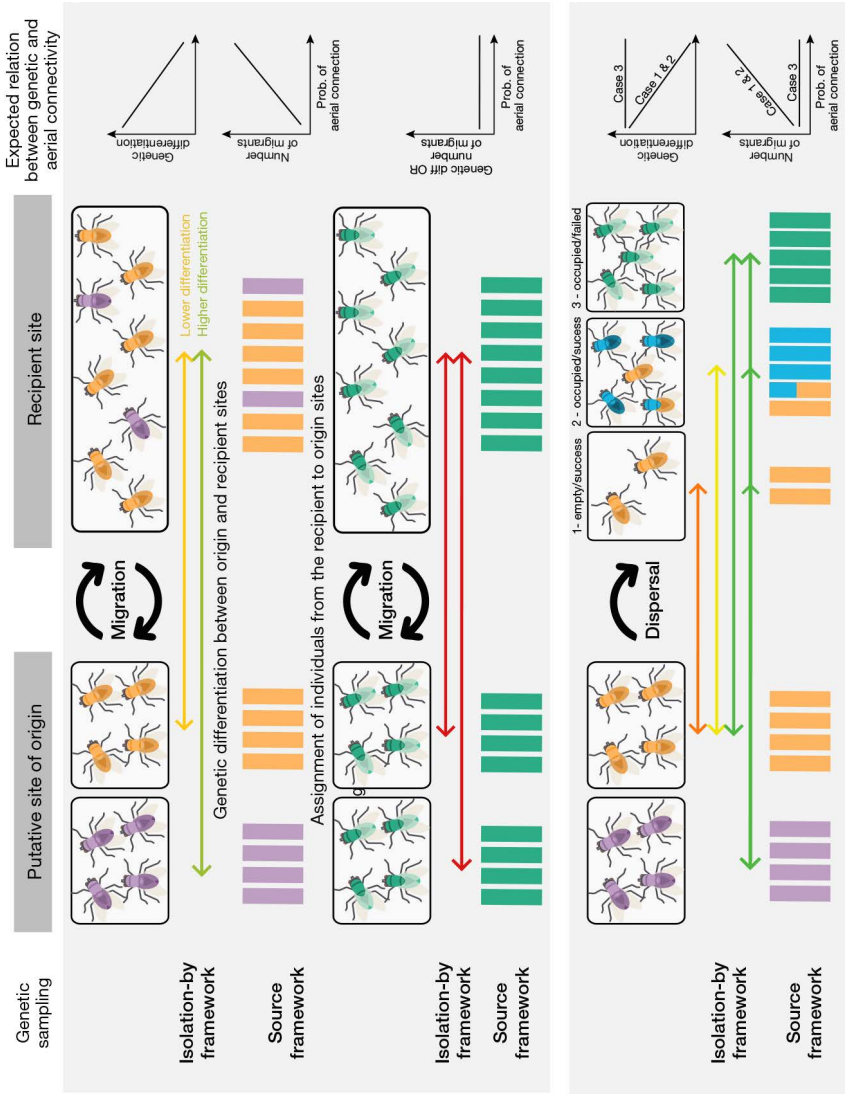

Figure 11.2. Illustration of the "isolation-by" and "source" frameworks under migration and dispersal scenarios.

Figure 11.2. In a round-trip migration (top panel), the timing of sampling can be crucial, as populations may travel massively between distant areas. When individuals migrate from genetically distinct populations to common feeding or overwintering grounds (with no reproduction), assignment techniques can allow for the detection of first-generation migrants, while differentiation measures based on allelic frequencies can blur the signal due to the mixing of individuals from different genetic sources in the recipient area. In the extreme case of migratory movement to a common breeding ground, source populations may be genetically too similar to detect any genetic signature, regardless of the method used. When dispersal (bottom panel) leads to the colonization of an empty habitat by a few individuals, the loss of genetic diversity (i.e. founder effect), compared to the source population, leads to differentiation, which can increase over time due to genetic drift, especially if the new population remains isolated. When dispersers integrate and reproduce within a previously established population, genetic differentiation between the source and recipient populations is expected to decrease. Finally, if dispersers fail to integrate into the recipient population, genetic differentiation is likely to remain high. In this case, assignment techniques can still be useful for tracing long-distance movements, provided that the migrants are sampled directly (i.e., first-generation migrants) before the disappearance of their genetic signature in the recipient population.

found that overwintering populations from the Indochinese Peninsula were the most likely source of long-distance immigrants to the temperate regions of China and Japan. Hu *et al.* (2024) also found that Indochina is probably the recipient of one-way LDD from South Asia and other regions of Southeast Asia. LDD events were visually associated with the main wind patterns: the southwest monsoon (January to September) and the inverted northeast winter monsoon (October to December), which could explain the roundtrip migration between Indochina and East Asia. Additionally, the West Pacific monsoon may support LDD from the Malay Archipelago to Indochina. Given the strong seasonality of the main wind currents and the round-trip movement of the brown planthopper, the timing of genetic sampling may be a key factor for maximizing the detection of real-time dispersers, as populations may travel massively between distant areas. In such a situation, the computation of spatio-temporal networks of aerial connectivity (as described in Choufany *et al.,* 2021) could allow the precise pinpointing of relevant spatio-temporal windows for genetic sampling. In addition, a statistically-based confrontation of such aerial connectivity networks with the genetic patterns of differentiation and gene flow could further strengthen conclusions on the geographical sources and aerial LDD pathways for the brown planthopper in Asia. As pointed out by Hereward *et al.* (2020), understanding source-sink dynamics, as observed between mainland South-East Asia and mainland China, would be key to ensure the efficiency of control measures at spatial scales coherent with the spatio-temporal dynamics of pest populations.

⏩ Conclusion

This chapter provides a brief overview of demographic and genetic approaches that can be used to assess the occurrence of wind-assisted LDD. Each of these approaches presents its own challenges, whether related to the feasibility of field implementation, underlying assumptions in data analysis and modelling, potential biases arising from sampling effort, tag loss in mark-recapture studies or the resolution of genetic markers. Direct approaches, such as marking and recapture of individuals, along with ground or aerial sampling, are among the most commonly used methods for estimating dispersal. However, when assessing long-distance wind-assisted dispersal, these methods face significant technical challenges due to the large spatial scales involved, which require sampling efforts that are logistically out of reach. For these reasons, marking and sampling techniques are sometimes combined with other methods including radar technologies, radio telemetry and remote sensing. For instance, the successive implementation of field and aerial surveys, marking techniques, radar technologies, and remote sensing to detect vegetation changes and identify breeding sites, has significantly enhanced the ability to predict swarm movements and provide early warnings of desert locust outbreaks. Integrating genetic-based methods can further improve estimates of long-distance dispersal, even when recapture rates are low or individuals are difficult to detect (Kim and Sappington, 2013), and can also provide reliable insights into both historical and contemporary connectivity of populations (see Chapuis *et al.* (2014, 2020) for examples on the desert locust). It is also worth noting that dedicated genetic methods can be used to trace colonization pathways and identify sources once a new taxon has successfully established in a new area. This is the aim of a whole field of research on biological invasions. The various methods and underlying challenges have been intensively reviewed including in agricultural settings where it can

help in designing appropriate pest management strategies to limit new introductions from the identified sources and entrance doors, for example Cristescu (2015); Estoup and Guillemaud (2010); Guillemaud *et al.* (2011); Lombaert *et al.* (2014); Picard *et al.* (2017); Sherpa and Després (2021).

In all cases, our ability to detect long-distance wind-assisted dispersal could be enhanced by first estimating windscapes (i.e., potential airborne connectivity networks) at the relevant spatial and temporal scales, before applying demographic, genetic, or integrated approaches. Indeed, spatial or spatio-temporal aerial connectivity networks provide crucial insights on the three phases of dispersal: the most likely source and recipient areas for the emigration and immigration phases, as well as the most probable atmospheric routes for the transfer phase, all within the time window considered. This knowledge allows for more targeted genetic sampling in likely source and recipient areas, and can, for instance, increase the effectiveness of aerial sampling by optimizing positioning and altitude of traps. Finally, it is important to remember that the establishment phase in a new habitat (i.e. the final phase of dispersal) may fail when local conditions (climate, resources, predation, competition, etc.) are not favorable, which means that some methods, notably based on genetic data, will not allow detection of individuals that indeed have travelled over long distances through air masses. However, environmental changes (e.g., landscape, climatic conditions and biological communities) or genetic changes (adaptation) may lead to future establishment, as long as the emigration and transfer phases of dispersal are successful. For monitoring purposes, suspected aerial pathways for LDD can guide global surveillance strategies and help anticipating introduction and/or spread of pathogens and insect vectors and pests (Bibard *et al.,* 2024a, 2024b; Soubeyrand *et al.,* 2024).

⏩ Literature cited

Abd El-Ghany N.M., *et al.*, 2020. A review: Application of remote sensing as a promising strategy for insect pests and diseases management. *Environ. Sci. Pollut. Res. Int.*, 27 (27), 33503-33515. https://doi.org/10.1007/s11356-020-09517-2

Acharya M., Thapa R., 2015. Remote sensing and its application in agricultural pest management. *J. Agric. Environ.*, 16, 43-61. https://doi.org/10.3126/aej.v16i0.19839

Adams R.H., *et al.*, 2019. Recent advances in the inference of gene flow from population genomic data. *Curr. Mol. Biol. Rep.*, 5 (3), 107-115. https://doi.org/10.1007/s40610-019-00120-0

Akhter T., *et al.*, 2023. Going places: Insect migration. *Resonance*, 28 (1), 71-84. https://doi.org/10.1007/s12045-023-1527-2

Alam A., *et al.*, 2023. Emerging trends in insect sex pheromones and traps for sustainable management of key agricultural pests in Asia: Beyond insecticides—a comprehensive review. *Int. J. Trop. Insect Sci.*, 43 (6), 1867-1882. https://doi.org/10.1007/s42690-023-01100-9

Alexander D.H., *et al.*, 2009. Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, 19 (9), 1655-1664. https://doi.org/10.1101/gr.094052.109

Asplen M.K., 2018. Dispersal strategies in terrestrial insects. *Curr. Opin. Insect Sci.*, 27, 16-20. https://doi.org/10.1016/j.cois.2018.01.009

Atieli H.E., *et al.*, 2023. Wind-assisted high-altitude dispersal of mosquitoes and other insects in East Africa. *J. Med. Entomol.*, 60 (4), 698-707. https://doi.org/10.1093/jme/tjad033

Badia-Boher J.A., *et al.*, 2023. Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark-recapture analyses. *Sci. Rep.*, 13 (1), 6970. https://doi.org/10.1038/s41598-023-32866-0

Baguette M., 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography*, 26 (2), 153-160. https://doi.org/10.1034/j.1600-0587.2003.03364.x

Balkenhol N., *et al.*, 2009. Statistical approaches in landscape genetics: An evaluation of methods for linking landscape and genetic data. *Ecography*, 32 (5), 818-830. https://doi.org/10.1111/j.1600-0587.2009.05807.x

Bauer S., *et al.*, 2019. The grand challenges of migration ecology that radar aeroecology can help answer. *Ecography*, 42 (5), 861-875. https://doi.org/10.1111/ecog.04083

Bauer S., *et al.*, 2024. Monitoring aerial insect biodiversity: A radar perspective. *Philos. Trans. R Soc. Lond. B Biol. Sci.*, 379 (1904), 20230113. https://doi.org/10.1098/rstb.2023.0113

Becciu P., *et al.*, 2019. Environmental effects on flying migrants revealed by radar. *Ecography*, 42 (5), 942-955. https://doi.org/10.1111/ecog.03995

Berry R.E., Taylor L.R., 1968. High-altitude migration of aphids in maritime and continental climates. *J. Anim. Ecol.*, 37 (3), 713. https://doi.org/10.2307/3084

Bibard A., *et al.*, 2024a. Quantitative risk assessment for the introduction of bluetongue virus into mainland Europe by long-distance wind dispersal of *Culicoides* spp.: A case study from Sardinia. *Risk Analysis*, risa.14345. https://doi.org/10.1111/risa.14345

Bibard A., *et al.*, 2024b. Assessing the risk of windborne dispersal of *Culicoides* midges in emerging epizootic hemorrhagic disease virus outbreaks in France. *Transbound. Emerg. Dis.*, 2024 (1), 5571195. https://doi.org/10.1155/2024/5571195

Bjerge K., *et al.*, 2021. An automated light trap to monitor moths (Lepidoptera) using computer vision-based tracking and deep learning. *Sensors*, 21 (2), 343. https://doi.org/10.3390/s21020343

Brown J.K.M., Hovmøller M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science*, 297 (5581), 537-541. https://doi.org/10.1126/science.1072678

Bryan N.C., *et al.*, 2019. Abundance and survival of microbial aerosols in the troposphere and stratosphere. *ISME J.*, 13 (11), 2789-2799. https://doi.org/10.1038/s41396-019-0474-0

Burgin L.E., *et al.*, 2013. Investigating incursions of Bluetongue virus using a model of long-distance *Culicoides* biting midge dispersal: Investigating Bluetongue virus incursions. *Transbound. Emerg. Dis.*, 60 (3), 263-272. https://doi.org/10.1111/j.1865-1682.2012.01345.x

Cain M.L., *et al.*, 2003. Long-distance dispersal. *Ecological Society of America*, 83, 1943-1944. https://doi.org/10.1890/01-0614

Caumette C., *et al.*, 2024. Hierarchizing multi-scale environmental effects on agricultural pest population dynamics: A case study on the annual onset of Bactrocera dorsalis population growth in Senegalese orchards. *Peer Community Journal*, 4e65. https://doi.org/10.24072/pcjournal.438

Cayuela H., *et al.*, 2018. Demographic and genetic approaches to study dispersal in wild animal populations: A methodological review. *Mol. Ecol.*, 27 (20), 3976-4010. https://doi.org/10.1111/mec.14848

Chailleux A., *et al.*, 2021. Understanding *Bactrocera dorsalis* trapping to calibrate area-wide management. *J. Appl. Entomol.*, 145 (9), 831-840. https://doi.org/10.1111/jen.12897

Chapman J., *et al.*, 2004. An aerial netting study of insects migrating at high altitude over England. *Bull. Entomol. Res.*, 94 (2), 123-136. https://doi.org/10.1079/BER2004287

Chapuis M.-P., *et al.*, 2011. Challenges to assessing connectivity between massive populations of the Australian plague locust. *Proc Biol Sci.*, 278 (1721), 3152-3160. https://doi.org/10.1098/rspb.2010.2605

Chapuis M., *et al.*, 2014. Demographic processes shaping genetic variation of the solitarious phase of the desert locust. *Mol. Ecol.*, 23 (7), 1749-1763. https://doi.org/10.1111/mec.12687

Chapuis M., *et al.*, 2020. A young age of subspecific divergence in the desert locust inferred by ABC random forest. *Mol. Ecol.*, 29 (23), 4542-4558. https://doi.org/10.1111/mec.15663

Choufany M., *et al.*, 2021. Spatiotemporal large-scale networks shaped by air mass movements. *Front. Appl. Math. Stat.*, 6, 602621. https://doi.org/10.3389/fams.2020.602621

Cocu N., *et al.*, 2005. Geographical location, climate and land use influences on the phenology and numbers of the aphid, *Myzus persicae*, in Europe: Environmental influences on aphid distribution. *J. Biogeogr.*, 32 (4), 615-632. https://doi.org/10.1111/j.1365-2699.2005.01190.x

Cornuet J.-M., *et al.*, 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics*, 153 (4), 1989-2000. https://doi.org/10.1093/genetics/153.4.1989

Cristescu M.E., 2015. Genetic reconstructions of invasion history. *Mol. Ecol.*, 24 (9), 2212-2225. https://doi.org/10.1111/mec.13117

Dadmal S.M., Khadakkar S., 2014. Insect faunal diversity collected through light trap at Akola vicinity of Maharashtra with reference to Scarabaeidae of Coleoptera. *J. Entomol. Zool. Stud.*, 2 (3), 44-48. https://www.entomoljournal.com/archives/2014/vol2issue3/PartA/18.pdf

Daniel Kissling W., *et al.*, 2014. Challenges and prospects in the telemetry of insects. *Biol. Rev. Camb. Philos Soc.*, 89 (3), 511-530. https://doi.org/10.1111/brv.12065

Dantart J., *et al.*, 2009. Long-distance wind-borne dispersal of the moth *Cornifrons ulceratalis* (Lepidoptera: Crambidae: Evergestinae) into the northern Mediterranean. *Eur. J. Entomol.*, 106 (2), 225-229. https://doi.org/10.14411/eje.2009.030

Datsugwai Mohammed S.S., Balogu T.V., 2023. Sampling methods for airborne microorganisms. *In:* Ilori M.O. *et al.*, (eds), *Aeromicrobiology*, Academic Press, Elsevier, 89-116. https://doi.org/10.1016/B978-0-323-96122-6.00001-3

Deblauwe I., *et al.*, 2022. From a long-distance threat to the invasion front: A review of the invasive *Aedes* mosquito species in Belgium between 2007 and 2020. *Parasit. Vectors*, 15 (1), 206. https://doi.org/10.1186/s13071-022-05303-w

Diniz-Filho J.A.F., *et al.*, 2013. Mantel test in population genetics. *Genet. Mol. Biol.*, 36 (4), 475-485. https://doi.org/10.1590/S1415-47572013000400002

Dufresnes C., *et al.*, 2023. Inferring genetic structure when there is little: Population genetics versus genomics of the threatened bat *Miniopterus schreibersii* across Europe. *Sci. Rep.*, 13 (1), 1523. https://doi.org/10.1038/s41598-023-27988-4

Eagles D., *et al.*, 2014. Long-distance aerial dispersal modelling of *Culicoides* biting midges: Case studies of incursions into Australia. *BMC Vet. Res.*, 10 (1), 135. https://doi.org/10.1186/1746-6148-10-135

Estoup A., Guillemaud T., 2010. Reconstructing routes of invasion using genetic data: Why, how and so what? *Mol. Ecol.*, 19 (19), 4113-4130. https://doi.org/10.1111/j.1365-294X.2010.04773.x

Flores D., *et al.*, 2009. Abundance of Asian citrus psyllid on yellow sticky traps in Florida, Puerto Rico, and Texas citrus groves. *Southwestern Entomologist*, 34 (1), 1-11. https://doi.org/10.3958/059.034.0101

Florio J., *et al.*, 2020. Massive windborne migration of Sahelian insects: Diversity, seasonality, altitude, and direction. *bioRxiv*, 2020.02.28.960195. https://doi.org/10.1101/2020.02.28.960195

Gandiaga F., James P.M.A., 2023. Quantifying long-distance dispersal of an outbreaking insect species using trap capture data and phenology. *Forest Ecology and Management*, 544, 121187. https://doi.org/10.1016/j.foreco.2023.121187

Gao G., *et al.*, 2016. Different thermal responses in two coexisting aphids may account for differences in their seasonal abundance in cotton fields. *Int. J. Pest Manage.*, 62 (4), 288-294. https://doi.org/10.1080/09670874.2016.1185551

Gao B., *et al.*, 2020. The 'migratory connectivity' concept, and its applicability to insect migrants. *Movement Ecology*, 8 (1), 48. https://doi.org/10.1186/s40462-020-00235-5

Gautier M., *et al.*, 2022. f-Statistics estimation and admixture graph construction with Pool-Seq or allele count data using the R package poolfstat. *Mol. Ecol. Resour*, 22 (4), 1394-1416. https://doi.org/10.1111/1755-0998.13557

Gillespie R.G., *et al.*, 2012. Long-distance dispersal: A framework for hypothesis testing. *Trends Ecol. Evol.*, 27 (1), 47-56. https://doi.org/10.1016/j.tree.2011.08.009

Gorki J.L., *et al.*, 2024. Pollen metabarcoding reveals the origin and multigenerational migratory pathway of an intercontinental-scale butterfly outbreak. *Current Biology*, 34 (12), 2684-2692.e6. https://doi.org/10.1016/j.cub.2024.05.037

Greenslade A.F., *et al.*, 2020. Aerial psyllid (Hemiptera: Psylloidea) detection and monitoring using suction traps in Britain: Population observations, new species found and a revised British checklist. *Entomologist's Gazette*, 71 (3), 151-163. https://doi.org/10.31184/G00138894.713.1749

Greenslade A.F.C., *et al.*, 2021. High-altitude migration of Psylloidea (Hemiptera) over England. *Entomologist's Gazette*, 72 (3), 189-198. https://doi.org/10.31184/G00138894.723.1817

Greenstone M.H., *et al*., 1991. Sampling aerially dispersing arthropods: A high-volume, inexpensive, automobile- and aircraft-borne system. *J. Econ. Entomol.*, 84 (6), 1717-1724. https://doi.org/10.1093/jee/84.6.1717

Grinshpun S.A., *et al*., 2015. Sampling for airborne microorganisms. *In:* Yates M.V., *et al*. (eds), *Manual of Environmental Microbiology, Fourth Edition*, Washington, DC, USA, ASM Press, 3.2.2-1-3.2.2-17. https://doi.org/10.1128/9781555818821.ch3.2.2

Guillemaud T., *et al*., 2011. Biological invasions in agricultural settings: Insights from evolutionary biology and population genetics. *Comptes Rendus Biologies*, 334 (3), 237-246. https://doi.org/10.1016/j.crvi.2010.12.008

Guillot G., Rousset F., 2013. Dismantling the Mantel tests. *Methods in Ecology and Evolution*, 4 (4), 336-344. https://doi.org/10.1111/2041-210x.12018

Hagler J.R., Jackson C.G., 2001. Methods for marking insects: Current techniques and future prospects. *Annu. Rev. Entomol.*, 46 (1), 511-543. https://doi.org/10.1146/annurev.ento.46.1.511

Hanski I., 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. *In:* Clobert J., *et al.* (eds), *Dispersal*, Oxford University Press, 283-298. https://doi.org/10.1093/oso/9780198506607.003.0022

Harrington R., 2001. EXAMINE (EXploitation of Aphid Monitoring In Europe): An European thematic network for the study of global change impacts on aphids, Proceedings 6th International Symposium on Aphids: Aphids in a New Millennium, Rennes, 3-7 September 2001. 45-49.

Harrington R., Woiwod I., 2007. Foresight from Hindsight: The Rothamsted insect survey. *Outlooks on Pest Management*, 18 (1), 9-14. https://doi.org/10.1564/18feb03

Hereward J.P., *et al*., 2020. Migration dynamics of an important rice pest: The brown planthopper (*Nilaparvata lugens*) across Asia—Insights from population genomics. *Evol. Appl.*, 13 (9), 2449-2459. https://doi.org/10.1111/eva.13047

Hollinger S.E., *et al*., 1991. A helicopter-mounted isokinetic aerial insect sampler. *J. Econ. Entomol.*, 84 (2), 476-483. https://doi.org/10.1093/jee/84.2.476

Holsinger K.E., Weir B.S., 2009. Genetics in geographically structured populations: Defining, estimating and interpreting FST. *Nat. Rev. Genet.*, 10 (9), 639-650. https://doi.org/10.1038/nrg2611

Hu G., *et al*., 2016. Mass seasonal bioflows of high-flying insect migrants. *Science*, 354 (6319), 1584-1587. https://doi.org/10.1126/science.aah4379

Hu Q.-L., *et al*., 2024. The genomic history and global migration of a windborne pest. *Science Advances*, 10 (17), eadk3852. https://doi.org/10.1126/sciadv.adk3852

Huang J., *et al*., 2024. Massive seasonal high-altitude migrations of nocturnal insects above the agricultural plains of East China. *Proc. Natl Acad. Sci. USA*, 121 (18), e2317646121. https://doi.org/10.1073/pnas.2317646121

Huestis D.L., *et al*., 2019. Windborne long-distance migration of malaria mosquitoes in the Sahel. *Nature*, 574 (7778), 404-408. https://doi.org/10.1038/s41586-019-1622-4

Irwin M.E., *et al*., 1988. Long-range aerial dispersal of cereal aphids as virus vectors in North America. *Philos. Trans. R. Soc. B Biol. Sci.*, 321 (1207), 421-446. https://doi.org/10.1098/rstb.1988.0101

Isard S.A., *et al*., 1990. Vertical distribution of aphids (Homoptera: Aphididae) in the planetary boundary layer. *Environ. Entomol.*, 19 (5), 1473-1484. https://doi.org/10.1093/ee/19.5.1473

Jacquet S., *et al*., 2016. Range expansion of the Bluetongue vector, *Culicoides imicola*, in continental France likely due to rare wind-transport events. *Sci. Rep.*, 6 (1), 27247. https://doi.org/10.1038/srep27247

Jombart T., 2008. *adegenet* : A R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24 (11), 1403-1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart T., *et al*., 2010. Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics*, 11 (1), 94. https://doi.org/10.1186/1471-2156-11-94

Jombart T., Ahmed I., 2011. *adegenet 1.3-1*: New tools for the analysis of genome-wide SNP data. *Bioinformatics*, 27 (21), 3070-3071. https://doi.org/10.1093/bioinformatics/btr521

Jones A., *et al*., 2007. The U.K. Met office's next-generation atmospheric dispersion model, NAME III. *In:* Borrego C., Norman A.-L. (eds), *Air pollution modeling and its application XVII*, Boston, MA, Springer US, 580-589. https://doi.org/10.1007/978-0-387-68854-1_62

Kim K.S., Sappington T.W., 2013. Population genetics strategies to characterize long-distance dispersal of insects. *Journal of Asia-Pacific Entomology*, 16 (1), 87-97. https://doi.org/10.1016/j.aspen.2012.11.004

Kling M.M., Ackerly D.D., 2021. Global wind patterns shape genetic differentiation, asymmetric gene flow, and genetic diversity in trees. *Proc. Natl Acad. Sci. USA*, 118 (17), e2017317118. https://doi.org/10.1073/pnas.2017317118

Kluiters G., *et al*., 2015. Local dispersal of palaearctic *Culicoides* biting midges estimated by mark-release-recapture. *Parasit. Vectors*, 8 (1), 86. https://doi.org/10.1186/s13071-015-0658-z

Knight S.M., *et al*., 2019. Radio-tracking reveals how wind and temperature influence the pace of daytime insect migration. *Biol. Lett.*, 15 (7), 20190327. https://doi.org/10.1098/rsbl.2019.0327

Koralewski T.E., *et al*., 2021. Modeling the dispersal of wind-borne pests: Sensitivity of infestation forecasts to uncertainty in parameterization of long-distance airborne dispersal. *Agric. For. Meteorol.*, 301-302, 108357. https://doi.org/10.1016/j.agrformet.2021.108357

Lawson D.J., *et al*., 2018. A tutorial on how not to over-interpret STRUCTURE and ADMIXTURE bar plots. *Nat. Comm.*, 9 (1), 3258. https://doi.org/10.1038/s41467-018-05257-7

Leyronas C., *et al*., 2018. Assessing the aerial interconnectivity of distant reservoirs of *Sclerotinia sclerotiorum*. *Front. Microbiol.*, 9, 2257. https://doi.org/10.3389/fmicb.2018.02257

Li Y., *et al*., 2023. Genomic analysis, trajectory tracking, and field surveys reveal sources and long-distance dispersal routes of wheat stripe rust pathogen in China. *Plant Communications*, 4 (4), 100563. https://doi.org/10.1016/j.xplc.2023.100563

Liebhold A.M., Tobin P.C., 2008. Population ecology of insect invasions and their management. *Annu. Rev. Entomol.*, 53 (1), 387-408. https://doi.org/10.1146/annurev.ento.52.110405.091401

Lindberg M.S., 2012. A review of designs for capture–mark–recapture studies in discrete time. *J. Ornithol.*, 152(S2), 355-370. https://doi.org/10.1007/s10336-010-0533-9

Löcken H., *et al*., 2020. 'Drone-netting' for sampling live insects. *J. Insect Sci.*, 20 (5), 3. https://doi.org/10.1093/jisesa/ieaa086

Lombaert E., *et al*., 2014. Complementarity of statistical treatments to reconstruct worldwide routes of invasion: The case of the Asian ladybird *Harmonia axyridis*. *Mol. Ecol.*, 23 (24), 5979-5997. https://doi.org/10.1111/mec.12989

Luquet M., *et al*., 2023. Predicting the seasonal flight activity of *Myzus persicae*, the main aphid vector of Virus Yellows in sugar beet. *Pest Manag. Sci.*, 79 (11), 4508-4520. https://doi.org/10.1002/ps.7653

Marko P.B., Hart M.W., 2011. The complex analytical landscape of gene flow inference. *Trends Ecol. Evol.*, 26 (9), 448-456. https://doi.org/10.1016/j.tree.2011.05.007

Matthysen E., 2012. Multicausality of dispersal: A review. *In:* Clobert J., *et al*. (eds), *Dispersal ecology and evolution*, Oxford University Press, 3-18. https://doi.org/10.1093/acprof:oso/9780199608898.003.0001

Meats A., Edgerton J.E., 2008. Short- and long-range dispersal of the Queensland fruit fly, *Bactrocera tryoni* and its relevance to invasive potential, sterile insect technique and surveillance trapping. *Australian Journal of Experimental Agriculture*, 48 (9), 1237. https://doi.org/10.1071/EA07291

Meats A., Smallridge C.J., 2007. Short- and long-range dispersal of medfly, *Ceratitis capitata* (Dipt., Tephritidae), and its invasive potential. *J. Appl. Entomol.*, 131 (8), 518-523. https://doi.org/10.1111/j.1439-0418.2007.01168.x

Menz M.H.M., *et al*., 2022. Individual tracking reveals long-distance flight-path control in a nocturnally migrating moth. *Science*, 377 (6607), 764-768. https://doi.org/10.1126/science.abn1663

Miao J., *et al*., 2013. Long-distance wind-borne dispersal of *Sitodiplosis mosellana* Géhin (Diptera: Cecidomyiidae) in Northern China. *J. Insect Behav.*, 26 (1), 120-129. https://doi.org/10.1007/s10905-012-9346-4

Morris C.E., *et al*., 2021. One Health concepts and challenges for surveillance, forecasting and mitigation of plant disease beyond the traditional scope of crop production. *Plant Pathology*, 86-97. https://doi.org/10.1111/ppa.13446

Mundt C.C., *et al*., 2009. Aerial dispersal and multiple-scale spread of epidemic disease. *EcoHealth*, 6 (4), 546-552. https://doi.org/10.1007/s10393-009-0251-z

Nathan R., *et al*., 2003. Methods for estimating long-distance dispersal. *Oikos*, 103 (2), 261-273. https://doi.org/10.1034/j.1600-0706.2003.12146.x

Nathan R., 2013. Dispersal biogeography. *In: Encyclopedia of biodiversity*, Elsevier, 539-561. https://doi.org/10.1016/B978-0-12-384719-5.00033-2

Noskov A., *et al*., 2021. A Review of insect monitoring approaches with special reference to radar techniques. *Sensors*, 21 (4), 1474. https://doi.org/10.3390/s21041474

Osborne J.L., *et al*., 2002. Monitoring insect dispersal: Methods and approaches. *In*: Bullock J.M., *et al.*, eds, *Dispersal Ecology*, Cambridge University Press, 24-49.

Otuka A., *et al*., 2019. Possible domestic dispersal of *Bactrocera dorsalis* during 2015 occurrence on the small islands of south-western Japan. *J. Appl. Entomol.*, 143 (5), 556-565. https://doi.org/10.1111/jen.12598

Paetkau D., *et al*., 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: A simulation-based exploration of accuracy and power. *Mol. Ecol.*, 13 (1), 55-65. https://doi.org/10.1046/j.1365-294X.2004.02008.x

Pflüger F.J., Balkenhol N., 2014. A plea for simultaneously considering matrix quality and local environmental conditions when analysing landscape impacts on effective dispersal. *Mol. Ecol.*, 23 (9), 2146-2156. https://doi.org/10.1111/mec.12712

Picard C., *et al*., 2017. Exploiting genetic information to trace plant virus dispersal in landscapes. *Annu. Rev. Phytopathol.*, 55 (1), 139-160. https://doi.org/10.1146/annurev-phyto-080516-035616

Prasad Y.G., Prabhakar M.P., 2012. Pest monitoring and forecasting. *In:* Abrol D.P., Shankar U. (eds), *Integrated pest management: principles and practice*, UK, CABI, 41-57. https://doi.org/10.1079/9781845938086.0041

Pritchard J.K., *et al*., 2000. Inference of population structure using multilocus genotype data. *Genetics*, 155 (2), 945-959. https://doi.org/10.1093/genetics/155.2.945

Raj A., *et al*., 2014. fastSTRUCTURE: Variational inference of population structure in large SNP data sets. *Genetics*, 197 (2), 573-589. https://doi.org/10.1534/genetics.114.164350

Reich M.S., *et al*., 2023. Metals and metal isotopes incorporation in insect wings: Implications for geolocation and pollution exposure. *Front. Ecol. Evol.*, 11, 1085903. https://doi.org/10.3389/fevo.2023.1085903

Reynolds D.R., *et al*., 2006. The migration of insect vectors of plant and animal viruses. *Advances in Virus Research*, 67, 453-517. https://doi.org/10.1016/S0065-3527(06)67012-7

Rezza G., 2014. Dengue and chikungunya: Long-distance spread and outbreaks in naïve areas. *Pathogens and Global Health*, 108 (8), 349-355. https://doi.org/10.1179/2047773214Y.0000000163

Rhodes M.W., *et al*., 2022. Recent advances in the remote sensing of insects. *Biological Reviews*, 97 (1), 343-360. https://doi.org/10.1111/brv.12802

Richard H., *et al*., 2023. Computing geographical networks generated by air-mass movement. *GeoHealth*, 7 (10), e2023GH000885. https://doi.org/10.1029/2023GH000885

Richardson J.L., *et al*., 2016. Navigating the pitfalls and promise of landscape genetics. *Mol. Ecol.*, 25 (4), 849-863. https://doi.org/10.1111/mec.13527

Riley J.R., 1992. A millimetric radar to study the flight of small insects. *Electronics & Communications Engineering Journal*, 4 (1), 43. https://doi.org/10.1049/ecej:19920011

Rodó X., *et al*., 2024. Microbial richness and air chemistry in aerosols above the PBL confirm 2,000-km long-distance transport of potential human pathogens. *Proc. Natl. Acad. Sci. USA*, 121 (38), e2404191121. https://doi.org/10.1073/pnas.2404191121

Rose D.J.W., *et al*., 2000. *The African Armyworm handbook: The status, biology, ecology, epidemiology and management of* Spodoptera exempta *(Lepidotera: Noctuidae)*, Natural Resources Institute, 304 p.

Ross P.A., *et al*., 2017. Wolbachia infections in *Aedes aegypti* differ markedly in their response to cyclical heat stress. *PLOS Pathog.*, 13 (1), e1006006. https://doi.org/10.1371/journal.ppat.1006006

Rousset F., 1997. Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics*, 145 (4), 1219-1228. https://doi.org/10.1093/genetics/145.4.1219

Rousset F., 1999. Genetic differentiation between individuals, *J. Evol. Biol.,* 13 (1), 58-62. https://doi.org/10.1046/j.1420-9101.2000.00137.x

Schmale D.G., Ross S.D., 2015. Highways in the sky: Scales of atmospheric transport of plant pathogens. *Annu. Rev. Phytopathol.*, 53 (1), 591-611. https://doi.org/10.1146/annurev-phyto-080614-115942

Schneider J.C., 1999. Dispersal of a highly vagile insect in a heterogeneous environment. *Ecology*, 80 (8), 2740-2749. https://doi.org/10.1890/0012-9658(1999)080[2740:DOAHVI]2.0.CO;2

Schoeny A., Gognalons P., 2020. Data on winged insect dynamics in melon crops in southeastern France. *Data Brief*, 29, 105132. https://doi.org/10.1016/j.dib.2020.105132

Sherpa S., Després L., 2021. The evolutionary dynamics of biological invasions: A multi-approach perspective. *Evol. Appl.*, 14 (6), 1463-1484. https://doi.org/10.1111/eva.13215

Showers W.B., *et al*., 1993. Mechanism of southward migration of a noctuid moth [*Agrotis Ipsilon* (Hufnagel)]: A complete migrant. *Ecology*, 74 (8), 2303-2314. https://doi.org/10.2307/1939583

Smith D.J., *et al*., 2018. Airborne bacteria in Earth's lower stratosphere resemble taxa detected in the troposphere: Results from a new NASA aircraft bioaerosol collector (ABC). *Front. Microbiol.*, 9, 01752. https://doi.org/10.3389/fmicb.2018.01752

Soubeyrand S., *et al*., 2024. Building integrated plant health surveillance: A proactive research agenda for anticipating and mitigating disease and pest emergence. *CABI Agric. Biosci.*, 5 (1), 72. https://doi.org/10.1186/s43170-024-00273-8

Stein A.F., *et al*., 2015. NOAA's HYSPLIT atmospheric transport and dispersion modeling system. *Bull. Am. Meteorol. Soc.*, 96 (12), 2059-2077. https://doi.org/10.1175/BAMS-D-14-00110.1

Sturtevant B.R., *et al*., 2013. Long-distance dispersal of spruce budworm (*Choristoneura fumiferana* Clemens) in Minnesota (USA) and Ontario (Canada) via the atmospheric pathway. *Agric. For. Meteorol.*, 168, 186-200. https://doi.org/10.1016/j.agrformet.2012.09.008

Sunde J., *et al*., 2020. Comparing the performance of microsatellites and RADseq in population genetic studies: Analysis of data for pike (*Esox lucius*) and a synthesis of previous studies. *Front. Genetics*, 11, 218. https://doi.org/10.3389/fgene.2020.00218

Sundqvist L., *et al*., 2016. Directional genetic differentiation and relative migration, *Ecol. Evol.*, 6 (11), 3461-3475. https://doi.org/10.1002/ece3.2096

Tatem A.J., *et al*., 2012. Air travel and vector-borne disease movement, *Parasitology*, 139 (14), 1816-1830. https://doi.org/10.1017/S0031182012000352

Taylor P.D., *et al*., 2017. The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement, *Avian Conservation and Ecology*, 12 (1), art8. https://doi.org/10.5751/ACE-00953-120108

Terui A., 2020. Modeling dispersal using capture–recapture data: A comparison of dispersal models. *Ecological Research*, 35 (5), 686-699. https://doi.org/10.1111/1440-1703.12168

Wang I.J., Bradburd G.S., 2014. Isolation by environment. *Mol. Ecol.*, 23 (23), 5649-5662. https://doi.org/10.1111/mec.12938

Waples R.S., *et al*., 2008. Integrating genetic data into management of marine resources: How can we do it better? *Fish and Fisheries*, 9 (4), 423-449. https://doi.org/10.1111/j.1467-2979.2008.00303.x

Westbrook J.K., *et al*., 2011. A model for long-distance dispersal of boll weevils (Coleoptera: Curculionidae). *Int. J. Biometeorol.*, 55 (4), 585-593. https://doi.org/10.1007/s00484-010-0359-4

Westbrook J., *et al*., 2016. Modeling seasonal migration of fall armyworm moths. *Int. J. Biometeorol.*, 60 (2), 255-267. https://doi.org/10.1007/s00484-015-1022-x

Whitlock M.C., Mccauley D.E., 1999. Indirect measures of gene flow and migration: FST not equal to 1/(4Nm + 1). *Heredity (Edinb)*, 82, 117-125. https://doi.org/10.1038/sj.hdy.6884960

Witzgall P., *et al*., 2010. Sex pheromones and their impact on pest management. *Journal of Chemical Ecology*, 36 (1), 80-100. https://doi.org/10.1007/s10886-009-9737-y

Wolda H., 1992. Trends in abundance of tropical forest insects. *Oecologia*, 89 (1), 47-52. https://doi.org/10.1007/BF00319014

Wright S., 1943. Isolation by distance. *Genetics*, 28, 114-138. https://doi.org/10.1093/genetics/28.2.114

Yaro A.S., *et al*., 2022. Diversity, composition, altitude, and seasonality of high-altitude windborne migrating mosquitoes in the Sahel: Implications for disease transmission. *Front Epidemiol*., 2, 1001782. https://doi.org/10.3389/fepid.2022.1001782

Zimmermann K., *et al*., 2011. Mark-recapture on large spatial scale reveals long distance dispersal in the Marsh Fritillary, *Euphydryas aurinia*. *Ecol. Entomol.*, 36 (4), 499-510. https://doi.org/10.1111/j.1365-2311.2011.01293.x

Chapter 12

Ecosystem invasion by airborne microorganisms

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Ecosystem invasion by airborne microorganisms represents a dynamic process that has shaped terrestrial and aquatic habitats for millennia. From the early days of aerobiology, researchers have explored how microorganisms become airborne, the sources and mechanisms behind their emission as aerosols, and how they spread through the atmosphere, often traversing vast distances and crossing ecological boundaries. Airborne microbes do not disperse uniformly but are influenced by vertical stratification, which creates distinct layers within the ensemble of microorganisms in Earth's atmosphere (referred to here as the aeromicrobiome) and affects their dispersal potential. Upon reaching a new habitat, microorganisms face selective pressures that influence whether they can successfully establish, survive, and affect local ecosystems. Yet, even introductions that are unsuccessful in terms of microbial reproduction may have immediate or delayed consequences on native microbial communities and broader ecosystem functions. Insights from both field and laboratory studies underscore the importance of understanding the outcome of these microbial immigrations (whether neutral, negative or beneficial). Here we refer to the ensemble of these outcomes of immigration as "invasions". The insights to be gained will offer valuable lessons about resilience, ecological interactions, and the often-overlooked influences of microbial hitchhikers on ecosystem health and stability.

⏩ Historical view of aerobiology

The concept of particle transport through the air has long been recognized. As early as 1676, Van Leeuwenhoek speculated about the presence of microscopic organisms in the air that are invisible to the naked eye (Van Leeuwenhoek, 1677). One of the earliest recorded instances of aerobiology sampling occurred in 1846, when Charles Darwin collected airborne dust aboard the HMS Beagle and identified various "organic forms" (Gorbushina *et al.*, 2007). In the 19th century, Pasteur (1860) was instrumental to the field through his work on cultivating microorganisms from the air to study the aerial dispersal and spread of bacterial pathogens. However, it wasn't until 1933 that F.C. Meier coined the term "aerobiology" when he described fungal spore samples collected by Charles and Anne Lindbergh during a flight over the Arctic (Meier and Lindbergh, 1935).

The first standardized, long-term aerobiology inventories were developed using the Hirst spore trap in 1952, an automated volumetric device that captures particles on a vaseline-coated microscope slide. This method, still widely used today for pollen monitoring, highlights the significance of pollen surveys in aerobiology due to their health implications (Hirst, 1952). With the well-established understanding that Saharan dust, along with biological particles, can travel vast distances and be deposited in distant environments (Chuvochina *et al.*, 2011; Greilinger *et al.*, 2018; Meola *et al.*, 2015; Peter *et al.*, 2014; Weil *et al.*, 2017), researchers have become increasingly interested in the possibility of contaminants and diseases being spread unintentionally or deliberately via the air (Brown and Hovmøller, 2002), hence the concept of ecosystem invasion or transfer.

The idea that global ecoregions share similar microbial communities suggests a form of microbial cosmopolitanism driven by environmental factors (Fenchel and Finlay, 2004; Kleinteich *et al.*, 2017; Nagler *et al.*, 2016). Airborne dispersal is considered one of the primary mechanisms for this distribution (Prospero *et al.*, 2005). In remote regions, airborne microorganisms and particles are often the main source of microbial and nutrient inputs (Maccario *et al.*, 2019; Keuschnig *et al.*, 2023). A well-known principle in microbial ecology, "Everything is everywhere, but the environment selects" (Becking, 1931), leads us to ask: "Is everything truly everywhere?" Molecular biology and advanced air sampling techniques now allow us to explore whether certain environmental filters –such as emissions from surfaces, survival in harsh atmospheric conditions (UV radiation, desiccation, extreme temperatures, low nutrients), and deposition processes– limit the successful long-range transport and establishment of biological particles in new environments. To better conceptualize how microorganisms disperse through the atmosphere, it is important to understand how the atmosphere is structured and the factors that lead to emissions and dispersal.

⏩ Sources of airborne microorganisms

The community composition within the atmosphere is highly variable and depends on the underlying ecosystems that act as seeding sources. Depending on when and where the sample is collected, primary biological aerosols (PBAs) make up between 13% and 74% of the global aerosol volume and include microorganisms such as bacteria, archaea, viruses, pollen, fungal spores, protists and propagules of algae and lichens. These PBAs can exist attached to inorganic particles, in aggregates, or independently in both the troposphere and stratosphere (Jones and Harrison, 2004; Jaenicke *et al.*, 2007; Burrows *et al.*, 2009b; Fröhlich-Nowoisky *et al.*, 2012; De Groot *et al.*, 2021).

Microorganisms are emitted into the atmosphere from a wide range of natural and anthropogenic sources, contributing to their abundance in the atmosphere (Womack *et al.*, 2010; Figure 12.1). Natural sources include soil, oceans, freshwater bodies, plants, and decaying organic matter, with soil dust and sea spray considered as the two most significant sources of aerosols, contributing approximately 1,500 teragrams (Tg) of global emissions each year (Burrows *et al.*, 2009a). The sea surface microlayer, which is the upper 200-400 micrometers of the ocean, contains high concentrations of microorganisms –up to 12 million per milliliter– making sea spray a significant producer of bioaerosols (Aller *et al.*, 2005; Wilson *et al.*, 2015). Chapter 7 presents more detail about the emissions of PBA from water surfaces. Soils, exhibiting high microbial diversity

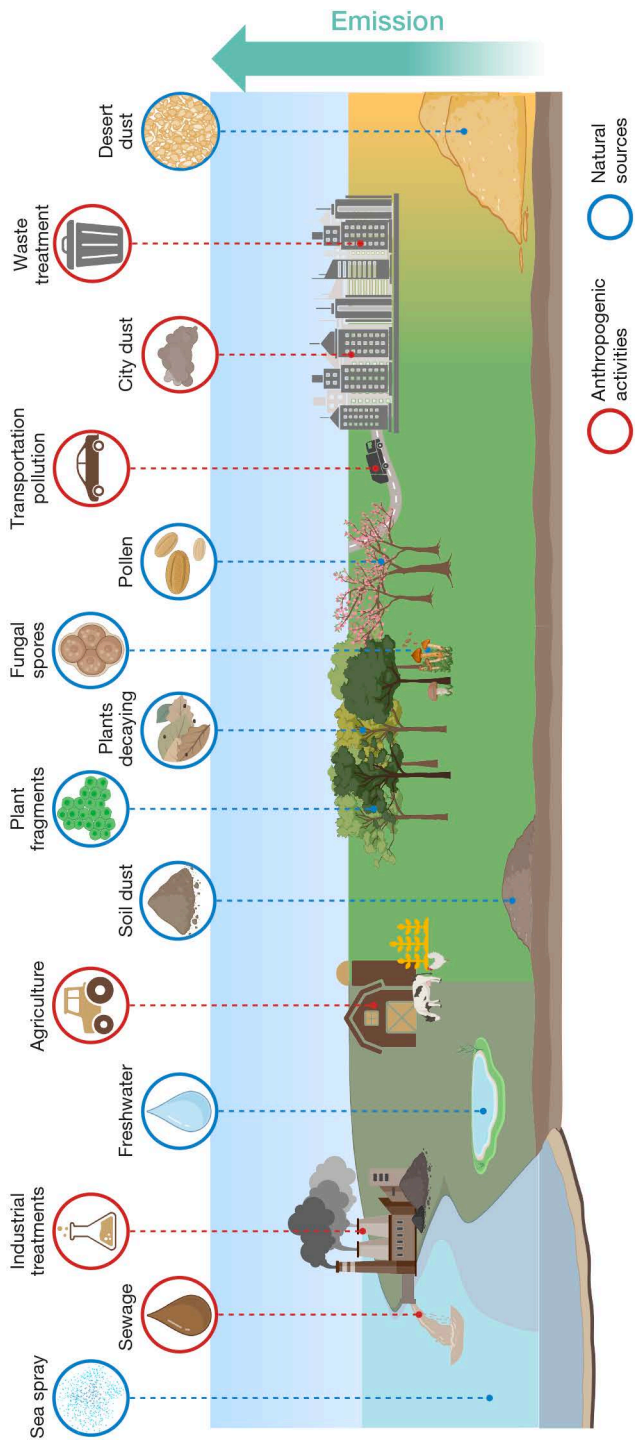

Figure 12.1. Global sources of airborne microorganisms. Created in BioRender (https://www.biorender.com).

(up to 30,000 species per gram of soil), also serve as major bioaerosol sources that release microorganisms to the atmosphere through processes like wind erosion and splashing (Curtis *et al.*, 2002; Gherboudj *et al.*, 2017; Huffman *et al.*, 2013; Joung *et al.*, 2017). Biological carriers such as pollen, fungal spores, and plant fragments also release microbes into the air. Anthropogenic activities, such as agriculture, industrial processes, and urbanization, contribute to microbial emissions from sewage, waste treatment facilities, and pollution. For example, the aeromicrobiome of indoor industrialized areas was generally dominated by bacteria, whereas natural outdoor environments were more dominated by fungi (Gusareva *et al.*, 2022). Since the composition of the atmosphere is tightly coupled to terrestrial surfaces, any changes to these surfaces due to shifts in global climate patterns for example, such as reduced Arctic sea ice, receding glaciers, and increased extreme weather events like storms and heavy rain, are expected to have significant but largely unquantified impacts on bioaerosol generation, abundance, and diversity (Bullard, 2013; Stroeve *et al.*, 2007).

⏩ Emissions of microorganisms

Emissions, the process by which microorganisms become airborne and can be considered to behave as aerosols, serves as the first major filter shaping the composition of airborne microbial communities (Tignat-Perrier *et al.*, 2020b). The mechanisms involved are described in more detail in Chapters 3, 7 and 8. This step influences the ratio of bacteria to fungi in the air, which generally favors bacteria, as observed through qPCR data. For instance, at high-altitude and suburban sites, the ratio of bacteria to fungi was about 10:1 and 6.5:1, respectively (Tanaka *et al.*, 2019), while in the soil, fungal biomass is generally higher than that of bacteria (1 to 5 times higher, on average, depending on the soil type; Djemiel *et al.*, 2023), suggesting that smaller bacterial cells are more easily aerosolized than larger fungal spores (Malik *et al.*, 2016).

Selective emissions may depend on various factors, such as cell size, physiological traits (e.g., cell membrane properties), and environmental conditions. For example, in the Amazon rainforest, Ascomycota fungi are more prevalent in the air than Basidiomycota, likely due to their smaller and lighter cell structures (Womack *et al.*, 2015). Similarly, bacterial taxa like Actinobacteria and lipid-enveloped viruses are more easily released from ocean surfaces due to their hydrophobic cell envelopes (Michaud *et al.*, 2018). Geng *et al.* (2024), studied the morphology of aerosols in air samples collected from Shanghai and suggested that Basidiomycota and Ascomycota fungal spores travel as independent atmospheric particles. Wind speed, surface conditions (e.g., soil moisture, plant cover), and meteorological factors like temperature and humidity also influence which microorganisms are successfully emitted into the atmosphere (Crandall and Gilbert, 2017; Górny and Ławniczek-Wałczyk, 2012; Womack *et al.*, 2015). Their aerodynamic properties then define the duration for which bioaerosols are able to remain suspended in turbulent air (Burrows *et al.*, 2009a, 2009b; Prospero *et al.*, 2005). The process of emission itself can be stressful and even lethal to microorganisms (Alsved *et al.*, 2018; Ng *et al.*, 2017, 2018; Thomas, 2013; Zhen *et al.*, 2013), and has been shown to induce stress responses such as antibiotic resistance gene transcription (Smith and King, 2023). Studies have shown that bacterial cells, such as *E. coli* and *Pseudomonas fluorescens*, often experience significant damage or death after a prolonged period as aerosols. Factors like

the speed of drying and environmental humidity also affect microbial survival rates, with ocean-sourced aerosols showing higher microbial survival compared to dry environments like soil.

Microorganisms are emitted into the atmosphere through a variety of natural and human-driven mechanisms (Burrows *et al.*, 2009b). Wind turbulence plays a major role in lifting bacteria from surfaces like soil, vegetation, and agricultural fields into the air, especially during events such as dust storms (Prospero *et al.*, 2005). Similarly, bubble-bursting at water surfaces, particularly in oceans and lakes, ejects microbial-containing droplets into the atmosphere (Michaud *et al.*, 2018; Aller *et al.*, 2005). Raindrops splashing on soil or plants can also dislodge microorganisms and allow them to become aerosols, as can volcanic activity, which expels ash and biological particles into the air. Human activities, including agriculture, construction, industrial processes and water treatment, mechanically disturb soil and surfaces, releasing microorganisms into the environment (Geng *et al.*, 2024). Weather phenomena, like thunderstorms and thermal convection, can then lift these organisms to higher atmospheric layers. Furthermore, human and animal respiration, coughing, and sneezing release microorganisms into the air, often in enclosed spaces.

Active emission mechanisms of microorganisms involve processes where microbes, particularly fungi and bacteria, play a direct role in their release into the air. For instance, many fungi actively discharge spores through specialized structures that use mechanical forces to propel spores into the atmosphere. This ejection can emit both the fungal spores and any bacteria attached to them into the atmosphere (Hassett *et al.*, 2015; Yafetto *et al.*, 2008). Similarly, certain bacteria possess mechanisms that promote emission, such as rapid desiccation tolerance, hydrophobic surface properties, and encapsulation within hydrated polysaccharide coatings (Michaud *et al.*, 2018). These active mechanisms often occur in environments rich in organic material, such as ocean surface waters, decaying plants or moist surfaces, where microbial populations thrive. Certain bacteria produce ice-nucleating and ice-binding proteins that allow them to catalyze ice formation (Hartmann *et al.*, 2022). This process is initiated on surfaces such as plant leaves or surface waters and aides in dissemination by mechanically disrupting biofilms or liquid films, creating fragments that can then enter the atmosphere where they become part of clouds and ice particles, influencing atmospheric processes (Morris *et al.*, 2004; Roeters *et al.*, 2021; Sahyoun *et al.*, 2017; Tesson and Šantl-Temkiv, 2018). This self-propulsion allows them to become airborne, aiding their dispersal across ecosystems, potentially impacting human health and environmental processes. Active mechanisms can be particularly effective in allowing microorganisms to evade adverse conditions, spread to new habitats, or colonize new hosts. Overall, emissions as aerosols is a critical selective process determining which microorganisms enter the atmosphere and how they are distributed.

⏩ Vertical stratification of the Earth's aeromicrobiome and implications for dispersal

Much like the ocean, the Earth's atmosphere is stratified. This layered structure of the atmosphere is crucial for regulating climate, supporting life, and shielding the Earth from harmful space radiation (Nicholson *et al.*, 2005). It is composed of several layers, each with distinct characteristics, primarily defined by changes in temperature, pressure, and

composition (Flohn and Penndorf, 1950). The layers, starting from the Earth's surface and extending outward into space, begin with the troposphere, the first layer where most of Earth's biosphere exists and all weather occurs (altitude range: 0 to ~8-15 km, varying with latitude, thicker at the equator and thinner at the poles, with temperature decreasing with altitude). Above this is the stratosphere, a relatively calm layer where intercontinental airplanes fly (altitude range: ~15 to 50 km, with temperature increasing with altitude), beyond which no life has been reported (Tignat-Perrier *et al.*, 2020b).

The layers in which most of the aeromicrobiome is found is the troposphere, and to a lesser extent, the stratosphere (Figure 12.2). The troposphere can be further divided into two main layers: the planetary boundary layer (PBL) and the free troposphere. Within the PBL, there is a specific sublayer called the Marine Boundary Layer (MBL), which is present over oceans and other large bodies of water and is influenced by

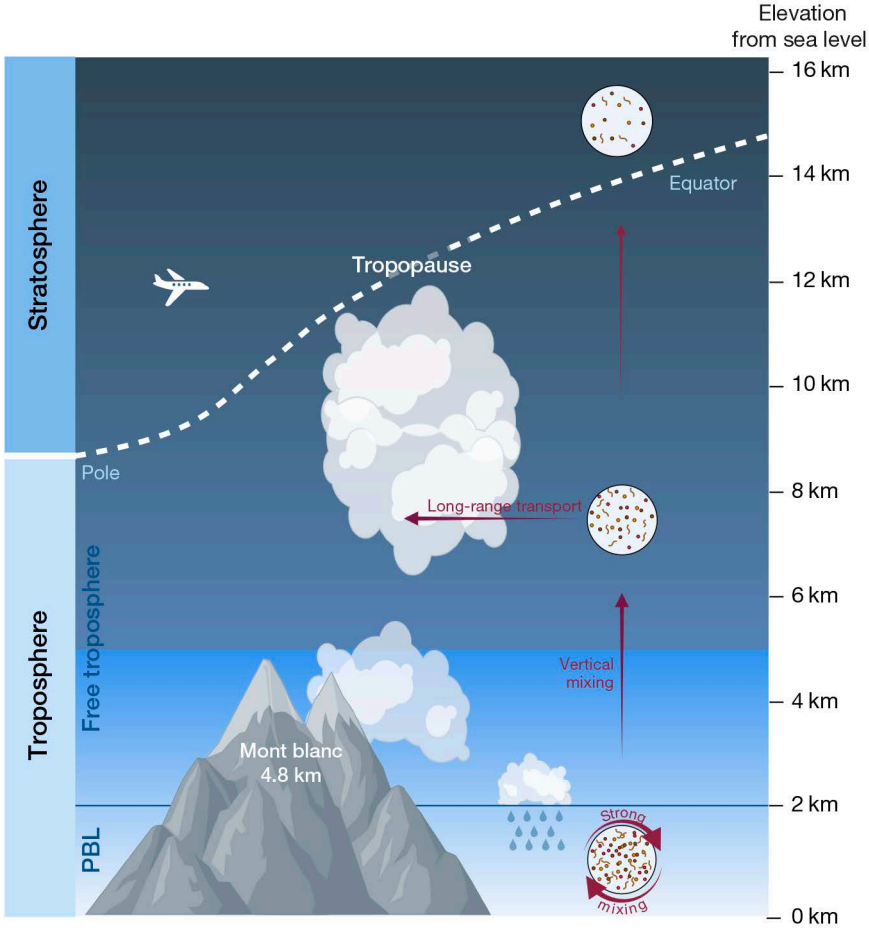

Figure 12.2. Vertical stratification and microbial abundance of Earth's atmosphere first layers and its impact on microbial dispersal. Free troposphere related studies: Tanaka *et al.* (2019), Zweifel *et al.* (2012), DeLeon-Rodriguez *et al.* (2013). Boundary layer related studies: Bertolini *et al.* (2013), Zhen *et al.* (2017), Genitsaris *et al.* (2017), Gandolfi *et al.* (2015), Cho and Hwang (2011), Park *et al.* (2018). Created in BioRender (https://www.biorender.com).

marine conditions, distinct from terrestrial boundaries. The PBL, as mentioned in Chapter 9, is the lowest part of the troposphere, directly influenced by Earth's surface, with varying height (100 m to 2 km) depending on time of day and weather. It is characterized by turbulence, strong vertical mixing, and the distribution of heat, moisture, and pollutants (Chan and Wood, 2013). It is also the layer with the highest density of microorganisms, ranging from 10^2 to 10^7 cells/m^3 of air. This is also the most dynamic layer in terms of microbial community structure and abundance. In samples collected from a tropical site, atmospheric microbial communities were shown to oscillate daily, in conjunction with temperature, relative humidity and CO_2 profiles. However, when sampled at the same time, communities were shown to be stable across days, weeks and months (Gusareva *et al.*, 2019). In temperate climates, diurnal patterns were also observed, but with a stronger winter/summer seasonal cycle (Gusareva *et al.*, 2020). Several studies have highlighted shifts in community structure in relation to changes in the underlying ecosystems, with a dominance of bacterial and fungal plant pathogens and wood rotting saprotrophs in the summer, and a lower biomass and dominance of bacteria in the winter (Tignat-Perrier *et al.*, 2020a; Gusareva *et al.*, 2020; Els *et al.*, 2019). Studies on the global fungal aeromicrobiome have shown that fungi follow highly predictable spatial and temporal dynamics, with seasonality in both species richness and community composition increasing with latitude (Abrego *et al.*, 2024).

In contrast, the free troposphere, which lies above the PBL and extends up to the tropopause (about 8–15 km), is more stable and less influenced by surface conditions, such as temperature variations (Drautz-Moses *et al.*, 2022). Air in the free troposphere flows smoothly with minimal turbulence, allowing for large-scale atmospheric circulation and transport of microorganisms. Rodó *et al.* (2024) confirmed the long-range transport (>2,000 km) of microorganisms, including pathogens and cells containing antibiotic resistance genes, from agricultural regions within the free troposphere. Reported cell numbers are lower in the free troposphere than in the PBL (Figure 12.2). In a study comparing PBL and free troposphere microbial communities, Els *et al.* (2019), reported that the genera found in high abundance in the free troposphere were mainly dominated by thermophilic, spore-forming Bacilli, which are globally widespread, along with generalist Planctomycetes and yeast formers (Jaing *et al.*, 2020), such as Ascomycota. Bacteria are also generally found in higher abundance than fungi (DeLeon-Rodriguez *et al.*, 2013), and the observed diel cycle of airborne microorganisms completely disappears (Drautz-Moses *et al.*, 2022). This pattern could either be the result of physical filtering based on particle size and density at the boundary of the PBL, or the selection of genera with specific resistance traits that enable them to survive in the free troposphere (DeLeon-Rodriguez *et al.*, 2013; Els *et al.*, 2019).

In the stratosphere, microbial cell counts drop significantly relative to the troposphere as a result of strong selection factors such as low temperature, oxygen, and humidity (DasSarma and DasSarma, 2018). Microorganisms enter the stratosphere through vertical air movements caused by events such as thunderstorms, dust storms, and volcanic eruptions. While exact numbers remain uncertain, sporulating and non-sporulating bacteria and fungi have been consistently detected, including extremophilic archaea and pathogenic bacteria that could potentially impact ecosystem health and functioning (DasSarma and DasSarma, 2018).

Understanding this stratification is critical when considering microbial dispersal, because the location of a given organism in the atmosphere will impact where and how far it is dispersed. For example, once an organism reaches higher layers of the atmosphere, it may enter more stable air currents, such as those found in the upper troposphere or stratosphere, which can facilitate smoother, long-range transport with minimal turbulence. As the climate changes, this will become even more critical, since a warmer atmosphere will result in a greater abundance of microorganisms reaching greater heights due to increased mixing leading to higher dispersal over larger distances (Drautz-Moses *et al.*, 2022).

⏩ Overview of microbial dispersal and deposition

At the landscape level, microorganisms are dispersed passively through the environment via various pathways. A dispersal route includes both the source of the microbial community (such as soil or sewage treatment plants) and the physical vector (like wind, ocean currents, or animal hosts) that transports individual cells (Walters *et al.*, 2022). Since microbial composition and abundance differ depending on the dispersal vector, the impact on resident microbial communities may be specific to each route (Barbour *et al.*, 2023). Once bacteria are emitted as aerosols, they travel via various mechanisms. Passive transport occurs via wind and turbulence, with bacteria remaining suspended in the atmosphere for extended periods. Vertical transport during thunderstorms, dust storms, and volcanic eruptions can lift bacteria into the troposphere and, under certain conditions, into the stratosphere. Bacteria often attach to dust particles, sea spray aerosols, or other particulate matter in the air, which can enhance their transport by providing a larger, more aerodynamic surface for dispersal.

Bacteria and bioaerosol particles in the atmosphere are subject to several deposition mechanisms that return them to the Earth's surface (Figure 12.3). Gravitational settling causes heavier particles to fall out of the atmosphere over time, but the small size of many bacteria allows them to remain suspended for longer, facilitating long-range transport (as described in Chapter 2). Wet deposition, through rain, snow, or fog, is one of the primary ways airborne bacteria are captured and brought back to land, plants, or water bodies. Under dry conditions, bacteria can settle by adhering to surfaces like vegetation, buildings, or soil. In samples collected within the free troposphere, Reche *et al.* (2018) determined that deposition rates for viruses ranged from 0.31 to 3.84 billion per square meter per day via atmospheric washout and from 0.26 to 3.89 billion through sedimentation. For bacteria, the rates varied from 0.88 to 5.78 million cells per square meter per day by washout, and from 0.55 to 2.80 million by sedimentation. Approximately 69% of the deposited viruses and 97% of the bacteria were found to be attached to dust or organic aggregates, indicating that airborne microorganisms predominantly adhere to these particles. Wet deposition is facilitated through the ability to nucleate ice (Reche *et al.*, 2018).

In summary, microorganisms are transported through a combination of natural and anthropogenic forces, with wind currents, weather events, and pollution influencing their journey. Once in the atmosphere, they can travel long distances and eventually settle back to Earth through deposition mechanisms like rain or gravitational settling. Environmental conditions and survival strategies, such as

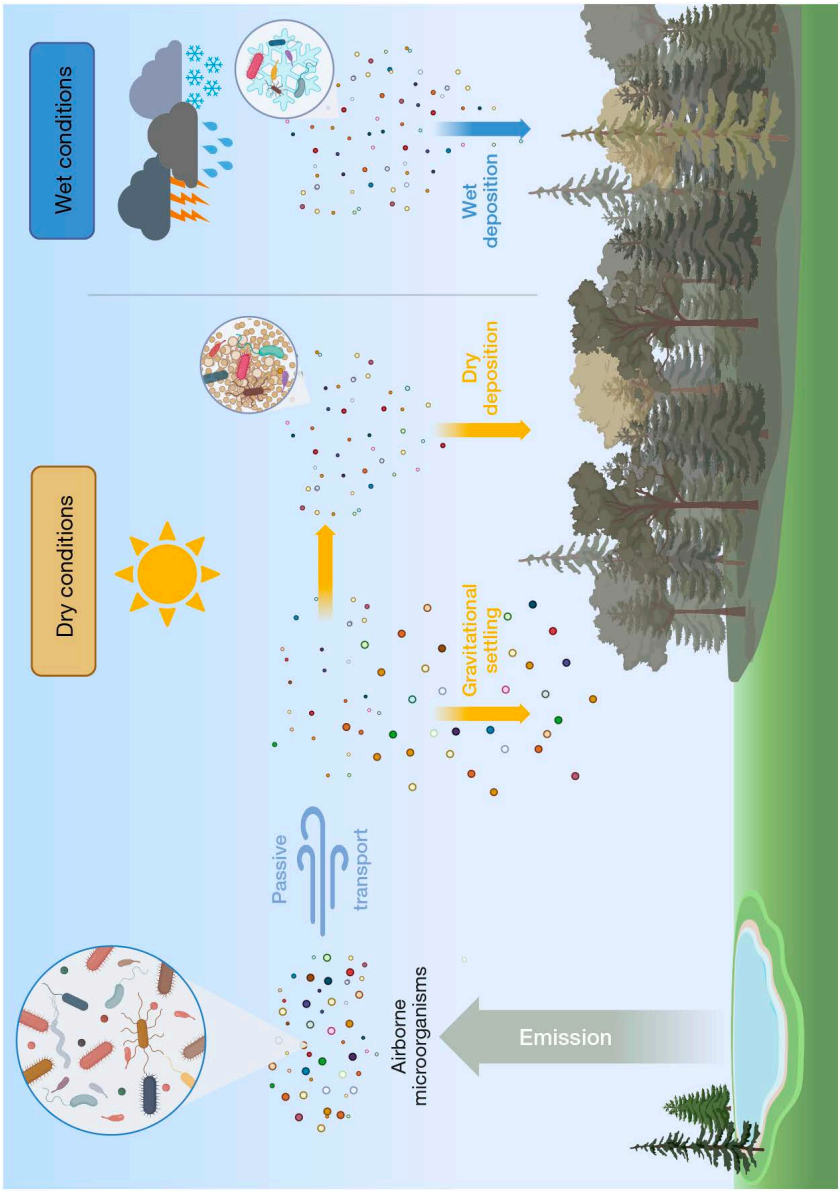

Figure 12.3. Microbial deposition from the atmosphere. Created in BioRender (https://www.biorender.com).

spore formation, play key roles in determining how long microorganisms remain airborne and where they eventually land.

What happens to microbial voyagers once they arrive at their destination?

As a result of emissions and atmospheric transport, microorganisms can disperse over various geographic distances, potentially colonizing new environments and impacting native microbial communities –a process known as microbial invasion (Liu and Salles, 2024a). This can be initiated by either a single strain or an entire microbial community, the latter referred to as community coalescence or community-driven invasion (Rillig *et al.*, 2015). This process plays a key role in shaping microbial community structure and influencing ecosystem functions. It encompasses four key mechanisms: dispersal, selection, diversification, and drift. However, few studies have specifically addressed the impact of atmospherically-transported microbial communities on the resident communities of the new ecosystems they potentially invade. This is owing to the complexity of source/sink relationships and the difficulty in using microorganisms as biological tracers through ecosystems.

Successful introduction

The population density of invasive species during transportation, along with their resilience to various abiotic stresses, plays a critical role in determining their likelihood of successful establishment and their subsequent ecological impacts (Martiny *et al.*, 2006; Pearson *et al.*, 2018). In some cases, the transport of microbial communities is obvious, for example via Saharan dust storms, characterized by high population densities that then deposit in remote locations, such as alpine ecosystems. Weil *et al.* (2017) compared microbes carried by Saharan dust storms and deposited in a snowpack in the dolomites to those in the underlying snow layers and soil. They identified members of the community that underwent long-distance transport through the troposphere, and postulated that some members were able to persist in Alpine soil following snowmelt. In a study on Alpine lakes, Saharan dust intrusion was shown to significantly alter both the chemical composition and the relative abundance of specific genera involved in important nutrient cycling processes in lake sediments (Castellano-Hinojosa *et al.*, 2024). Dust aerosols were also shown to deliver active bacteria to the ocean's surface that can reduce the diversity of marine bacterial population (Na *et al.*, 2023). These examples involve high-biomass seeding sources (Saharan dust events) that enter low-biomass systems, making it easy to identify source-sink relationships, however, this is less obvious when considering aeromicrobiomes outside of these types of events. For example, Zhou *et al.* (2021) conducted a controlled microcosm experiment to study the air-soil-phyllosphere continuum to determine the key seeding sources and contributors to the phyllosphere microbial community. Based on taxonomic comparisons, the air, soil and phyllosphere communities overlapped indicating interconnectedness, but the soil and phyllosphere were shown to contribute more to seeding the atmosphere than vice versa. The difficulty in teasing apart seeding sources might be related to the density of organisms in the atmosphere as compared to the soil and phyllosphere. Jones *et al.* (2008) also suggested a minimal role of atmospherically deposited organisms in structuring lake water communities.

⏩ Post-depositional selection and survival: Lessons from field and laboratory experiments

Another layer of complexity is determining whether these organisms are actually able to survive and colonize once they have been deposited. The successful invasion of a new ecosystem depends on the organisms' capacity to overcome multiple barriers, including environmental conditions, competition from established species, predation by larger organisms, and the formation of protective biofilms. Adverse abiotic factors like temperature and nutrient availability can hinder survival, while established communities can outcompete newcomers for resources. Additionally, predation by protozoa and chemical inhibitors, such as heavy metals, can further limit colonization. The immune responses in multicellular hosts also act as a barrier, and geographical isolation can restrict microbial dispersal.

Most of the relevant work related to this is from either extreme, oligotrophic environments, or controlled laboratory experiments. For example, snowpacks have recently gained attention as a useful model system for studying post-depositional selection. In Maccario *et al.* (2019), the microbial community composition of different layers of snow formed over sea-ice were compared to the atmosphere. The surface snow had a more similar microbial composition to the atmosphere as compared to deeper snow layers, suggesting that snowpack conditions select for specific microbial communities. This result is consistent with that of Els *et al.* (2020), who conducted a year-long survey at a high altitude site in the Alps to compare the community composition of the atmosphere to that of the underlying snowpack. Their results showed a higher similarity between the air and snow communities in the fall at the onset of snow accumulation, but that community overlap diminished as the season progressed. Keuschnig *et al.* (2023), applied the neutral model approach developed by Harris *et al.* (2017), to distinguish between stochastic and deterministic processes regulating how microbial communities assemble in the snow as a result of atmospheric deposition. The capacity to nucleate ice was shown to actively select for organisms into freshly fallen snow, but further analysis showed that these organisms were not successful over longer time scales, again supporting post-depositional selection and the role of abiotic factors in driving community assembly. The snowpack was also used in controlled laboratory experiments as a proxy for atmospheric deposition. Malard and Pearce (2022) showed that bacterial persistence of potential colonizers from the snow was lower in acidic and alkaline soils, as compared to acidoneutral soils. This would suggest that local soil properties might have a strong influence on the success of colonization. This is in line with other soil microcosm studies that showed that most invaders (99%) failed to survive (Liu and Salles, 2024b). These results might be driven by biotic factors such as competition and defense, since the rapid recruitment of airborne microorganisms was shown to successfully occur in sterilized soils (Fløistrup *et al.*, 2018).

Similar experiments have been carried out on surface waters. Using a mesocosm experiment, researchers found that bioaerosols, including airborne microorganisms and viruses, altered surface microbial diversity and productivity in low-nutrient, low-chlorophyll aquatic ecosystems (Mescioglu *et al.*, 2019). Dust containing viable organisms reduced primary production by up to 50% while increasing bacterial production by up to 55% as compared to dust treated to eliminate bioaerosols. These findings suggest that airborne microbes can significantly influence carbon cycling and nutrient

dynamics in oligotrophic regions. This is coherent with field data from oligotrophic surface waters (Rahav *et al.*, 2016a). In mesocosm experiments, Saharan dust was shown to rapidly increase N_2 fixation rates, contributing 3–8% to primary productivity in surface seawater (Rahav *et al.*, 2016b). In another experiment where Saharan dust enriched rainwater was added to sterilized high-altitude lake water, bacterial abundance was shown to increase 100 fold within 5 days (Peter *et al.*, 2014). This suggests that the organisms transported are not only viable, but can, in some cases, be a source of rare bacteria for freshwater ecosystems.

The results from these studies are derived from oligotrophic environments, where successful establishment might be facilitated due to lower competition from the resident community. Regardless of the outcome, they highlight the ability of aerial-transported organisms to successfully colonize and potentially impact other ecosystems.

The numerous impacts of invasion on ecosystems

Studies have shown that even transient invaders, which fail to establish long-term populations, can still leave lasting effects on the recipient community (Amor *et al.*, 2020). This can occur due to several factors. For example, if an invading community is lysed upon invasion, their cellular contents are released and can support the growth of neighboring live bacteria. The recipient community might also respond to the presence of dead cells by altered gene expression, such as the upregulation of motility- and chemotaxis-associated genes, amongst others (Steinhaus and Birkeland, 1939; Nioh and Furusaka, 1968; Smakman and Hall, 2022). Unsuccessful invaders are also able to influence the recipient community through various direct and indirect effects (Buchberger and Stockenreiter, 2018; Miller, 1994; Miller *et al.*, 2009). For example, invaders can alter the pH of their environment or release antibiotics, directly impacting some members of the recipient community and altering its structure (Amor *et al.*, 2020). If the invaders are able to compete more successfully for certain nutrients, they can indirectly impact the population density of some members of the community by altering the network of intra-community interactions (Abrams, 2004). This research shows that invasion impacts occur rapidly following the introduction of the invader, regardless of its ability to proliferate or spread (Mallon *et al.*, 2018; Xing *et al.*, 2021). Consequently, (i) it is plausible that community coalescence can have significant effects, even if some invasive species fail to establish, and (ii) the impacts on invaders and resident species should be viewed separately. Interactions between invaders and native bacteria occur, often involving suppression (Liu and Salles, 2024b), emphasizing the importance of microbial interactions during and after coalescence.

Whether colonization leads to the proliferation of invading species or not, it can also modify the genetic pool of ecosystems through the release of free DNA. Free DNA plays a crucial role in bacterial evolution through a process known as horizontal gene transfer (HGT) (Engelstädter and Moradigaravand, 2014), where genetic material is exchanged between organisms, bypassing traditional (vertical) inheritance. This extracellular DNA can be taken up by bacteria via transformation, allowing them to acquire new traits such as antibiotic resistance, metabolic capabilities, or virulence factors. The integration of free DNA into the bacterial genome facilitates rapid adaptation to environmental pressures and promotes genetic diversity. This mechanism is particularly important in microbial ecosystems, where constant exposure to stressors such as antibiotics or

changes in nutrient availability drive the need for fast evolutionary responses. The presence of free DNA in the environment can significantly accelerate bacterial evolution, contributing to the spread of advantageous genes across populations, enhancing survival and promoting long-term ecological and evolutionary success.

⏩ Conclusions and perspectives

The invasion of ecosystems by airborne microorganisms represents a significant, yet often overlooked, driver of ecological change. These microscopic organisms, including bacteria, fungi, viruses, and spores, are capable of traveling vast distances through the atmosphere and can colonize new environments, altering biodiversity, nutrient cycles, and even climate regulation processes. The ecological impacts of these invasions can be profound, affecting native species, soil and water quality, and plant health, while potentially introducing pathogens that disrupt existing ecosystems. For example, the aerial dispersal of pathogenic fungi such as *Cronartium ribicola* have been shown to reduce pine tree dominance in forests, while *Cryphonectria parasitica*, responsible for chestnut blight, has led to significant economic losses due to tree mortality (Thakur *et al.*, 2019).

As a future perspective, there is crucial need for a deeper understanding of the mechanisms behind airborne microbial dispersal, colonization, and establishment in new habitats. Global change factors, such as land-use modification, pollution, and alteration of temperature and precipitation regimes, are likely to influence the patterns and intensity of microbial invasions. Developments in molecular biology and remote sensing technologies offer new opportunities to track and identify microorganisms and their ecological effects. Recent improvements in the extraction and sequencing of low biomass samples enable researchers to pair omics and biogeochemical analyses from samples collected with automated sampling systems from air quality monitoring programs. Future research should use these advancements to observe how global change factors interact with airborne microbial communities to anticipate and mitigate potential ecological disruptions.

Finally, there is a pressing need for developing global monitoring networks to track the spread of invasive microorganisms and to assess their long-term impacts on ecosystem health and stability. Such efforts would not only enhance our understanding of microbial biogeography but also inform conservation strategies aimed at preserving biodiversity in the face of increasing biological invasions. Chapter 14 presents strategies for delimiting the regional and global scopes needed for these monitoring networks.

⏩ Literature cited

Abrams P.A., 2004. Trait-initiated indirect effects due to changes in consumption rates in simple food webs. *Ecology*, 85 (4), 1029-1038. https://doi.org/10.1890/03-0501

Abrego N., *et al.*, 2024. Airborne DNA reveals predictable spatial and seasonal dynamics of fungi. *Nature*, 631 (8022), 835-842.

Aller J.Y., *et al.*, 2005. The sea surface microlayer as a source of viral and bacterial enrichment in marine aerosols. *J. Aerosol Sci.*, 36 (5), 801-812. https://doi.org/10.1016/j.jaerosci.2004.10.012

Alsved M., *et al.*, 2018. Effect of aerosolization and drying on the viability of *Pseudomonas syringae* cells. *Front. Microbiol.*, 93086. https://doi.org/10.3389/fmicb.2018.03086

Amor D.R., *et al.*, 2020. Transient invaders can induce shifts between alternative stable states of microbial communities. *Science Advances*, 6 (8), eaay8676. https://doi.org/10.1126/sciadv.aay8676

Barbour K.M., *et al*., 2023. Towards quantifying microbial dispersal in the environment. *Environ. Microbiol.*, 25 (1), 137-142. https://doi.org/10.1111/1462-2920.16270

Becking L.G.M.B., 1931. Gaia of leven en aarde. *Oratie gewoon hoogleraar, Rijksuniv. Leiden, Mart. Nijhoff's Gravenhage,* 1–20. https://doi.org/10.1007/978-94-011-9114-2_1

Bertolini V., *et al*., 2013. Temporal variability and effect of environmental variables on airborne bacterial communities in an urban area of Northern Italy. *Appl. Microbiol. Biotechnol.*, 97 (14), 6561-6570. https://doi.org/10.1007/s00253-012-4450-0

Brown J.K.M., Hovmøller M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science*, 297 (5581), 537-541. https://doi.org/10.1126/science.1072678

Buchberger F., Stockenreiter M., 2018. Unsuccessful invaders structure a natural freshwater phytoplankton community. *Ecosphere*, 9 (3), e02158. https://doi.org/10.1002/ecs2.2158

Bullard J.E., 2013. Contemporary glacigenic inputs to the dust cycle. *Earth Surface Processes and Landforms*, 38 (1), 71-89. https://doi.org/10.1002/esp.3315

Burrows S.M., *et al*., 2009a. Bacteria in the global atmosphere – Part 2: Modeling of emissions and transport between different ecosystems. *Atmos. Chem. Phys.*, 9 (23), 9281-9297. https://doi.org/10.5194/acp-9-9281-2009

Burrows S.M., *et al*., 2009b. Bacteria in the global atmosphere – Part 1: Review and synthesis of literature data for different ecosystems. *Atmos. Chem. Phys.*, 9, 9263–9280. https://doi.org/10.5194/acp-9-9263-2009

Castellano-Hinojosa A., *et al*., 2024. Strong Saharan dust deposition events alter microbial diversity and composition in sediments of high-mountain lakes of Sierra Nevada (Spain). *Microb. Ecol.*, 87 (1), 99. https://doi.org/10.1007/s00248-024-02416-w

Chan K.M., Wood R., 2013. The seasonal cycle of planetary boundary layer depth determined using COSMIC radio occultation data. *J. Geophys. Res.: Atmospheres*, 118 (22), 12,422-12,434. https://doi.org/10.1002/2013JD020147

Cho B.C., Hwang C.Y., 2011. Prokaryotic abundance and 16S rRNA gene sequences detected in marine aerosols on the East Sea (Korea), Prokaryotes above the East Sea. *FEMS Microbiol. Ecol.*, 76 (2), 327-341. https://doi.org/10.1111/j.1574-6941.2011.01053.x

Chuvochina M.S., *et al*., 2011. Community variability of bacteria in alpine snow (Mont Blanc) containing saharan dust deposition and their snow colonisation potential. *Microbes Environ.*, 26 (3), 237-247. https://doi.org/10.1264/jsme2.ME11116

Crandall S.G., Gilbert G.S., 2017. Meteorological factors associated with abundance of airborne fungal spores over natural vegetation. *Atmos. Environ.*, 162, 87-99. https://doi.org/10.1016/j.atmosenv.2017.05.018

Curtis T.P., *et al*., 2002. Estimating prokaryotic diversity and its limits. *Proc. Natl Acad. Sci. USA*, 99 (16), 10494-10499. https://doi.org/10.1073/pnas.142680199

DasSarma P., DasSarma S., 2018. Survival of microbes in Earth's stratosphere. *Curr. Opin. Microbiol.*, 43, 24-30. https://doi.org/10.1016/j.mib.2017.11.002

De Groot G.A., *et al*., 2021. The aerobiome uncovered: Multi-marker metabarcoding reveals potential drivers of turn-over in the full microbial community in the air. *Environ. Int.*, 154, 106551. https://doi.org/10.1016/j.envint.2021.106551

DeLeon-Rodriguez N., *et al*., 2013. Microbiome of the upper troposphere: Species composition and prevalence, effects of tropical storms, and atmospheric implications. *Proc. Natl Acad. Sci. USA*, 110 (7), 2575-2580. https://doi.org/10.1073/pnas.1212089110

Djemiel C., *et al*., 2023. Biogeographical patterns of the soil fungal:bacterial ratio across France, *mSphere*, 8 (5), e00365-23. https://doi.org/10.1128/msphere.00365-23

Drautz-Moses D.I., *et al*., 2022. Vertical stratification of the air microbiome in the lower troposphere. *Proc. Natl Acad. Sci. USA*, 119 (7), e2117293119. https://doi.org/10.1073/pnas.211729311

Els N., *et al*., 2019. Beyond the planetary boundary layer: Bacterial and fungal vertical biogeography at Mount Sonnblick, Austria. *Geo: Geography and Environment*, 6 (1), e00069. https://doi.org/10.1002/geo2.69

Els N., *et al*., 2020. Comparison of bacterial and fungal composition and their chemical interaction in free tropospheric air and snow over an entire winter season at Mount Sonnblick, Austria. *Front. Microbiol.*, 11980. https://doi.org/10.3389/fmicb.2020.00980

Engelstädter J., Moradigaravand D., 2014. Adaptation through genetic time travel? Fluctuating selection can drive the evolution of bacterial transformation. *Proc. Biol. Sci.*, 281 (1775), 20132609. https://doi.org/10.1098/rspb.2013.2609

Fenchel T., Finlay B.J., 2004. The ubiquity of small species: Patterns of local and global diversity. *BioScience*, 54 (8), 777. https://doi.org/10.1641/0006-3568(2004)054[0777:TUOSSP]2.0.CO;2

Flohn H., Penndorf R., 1950. The stratification of the atmosphere 1 (I). *Bull. Am. Meteorol. Soc.*, 31 (3), 71-78. https://doi.org/10.1175/1520-0477-31.3.71

Fløistrup K.M., *et al*., 2018. Recruitment of airborne microorganisms on sterilized soil at different heights above ground. *Applied Soil Ecology*, 12685-87. https://doi.org/10.1016/j.apsoil.2018.02.011

Fröhlich-Nowoisky J., *et al*., 2012. Biogeography in the air: Fungal diversity over land and oceans. *Biogeosciences*, 9 (3), 1125-1136. https://doi.org/10.5194/bg-9-1125-2012

Gandolfi I., *et al.*, 2015. Spatio-temporal variability of airborne bacterial communities and their correlation with particulate matter chemical composition across two urban areas. *Appl. Microbiol. Biotechnol.*, 99 (11), 4867-4877. https://doi.org/10.1007/s00253-014-6348-5

Geng X., *et al*., 2024. Nycterohemeral airborne fungal and bacterial communities and health risks of potential pathogens in Shanghai. *Environmental Science: Atmospheres*, 4 (2), 190-201. https://doi.org/10.1039/D3EA00141E

Genitsaris S., *et al*., 2017. Variability of airborne bacteria in an urban Mediterranean area (Thessaloniki, Greece). *Atmos. Environ.*, 157, 101-110. https://doi.org/10.1016/j.atmosenv.2017.03.018

Gherboudj I., *et al*., 2017. Identifying natural dust source regions over the Middle-East and North-Africa: Estimation of dust emission potential. *Earth-Science Reviews*, 165, 342-355. https://doi.org/10.1016/j.earscirev.2016.12.010

Gorbushina A.A., *et al*., 2007. Life in Darwin's dust: Intercontinental transport and survival of microbes in the nineteenth century. *Environ. Microbiol.*, 9 (12), 2911-2922. https://doi.org/10.1111/j.1462-2920.2007.01461.x

Górny R.L., Ławniczek-Wałczyk A., 2012. Effect of two aerosolization methods on the release of fungal propagules from a contaminated agar surface. *Ann. Agric. Environ. Med.*, 19 (2), 279-84.

Greilinger M., *et al*., 2018. Contribution of saharan dust to ion deposition loads of high alpine snow packs in Austria (1987–2017). *Front. Earth Sci.*, 6126. https://doi.org/10.3389/feart.2018.00126

Gusareva E.S., *et al*., 2019. Microbial communities in the tropical air ecosystem follow a precise diel cycle. *Proc. Natl Acad. Sci. USA*, 116 (46), 23299-23308. https://doi.org/10.1073/pnas.1908493116

Gusareva E.S., *et al*., 2020. Taxonomic composition and seasonal dynamics of the air microbiome in West Siberia. *Sci. Rep.*, 10 (1), 21515. https://doi.org/10.1038/s41598-020-78604-8

Gusareva E.S., *et al*., 2022. Short-range contributions of local sources to ambient air. *Proc. Natl Acad. Sci. USA Nexus*, 1 (2), pgac043. https://doi.org/10.1093/pnasnexus/pgac043

Harris K., *et al*., 2017. Linking statistical and ecological theory: Hubbell's unified neutral theory of biodiversity as a hierarchical Dirichlet process. *Proceedings of the IEEE*, 105 (3), 516-529. https://doi.org/10.1109/JPROC.2015.2428213

Hartmann S., *et al*., 2022. Structure and protein-protein interactions of ice nucleation proteins drive their activity. *Front. Microbiol.*, 13, 872306. https://doi.org/10.3389/fmicb.2022.872306

Hassett M.O., *et al*., 2015. Mushrooms as rainmakers: How spores act as nuclei for raindrops. *PLOS ONE*, 10 (10), e0140407. https://doi.org/10.1371/journal.pone.0140407

Hirst J.M., 1952. An automatic volumetric spore trap. *Ann. Appl. Biol.*, 39 (2), 257-265. https://doi.org/10.1111/j.1744-7348.1952.tb00904.x

Huffman J.A., *et al*., 2013. High concentrations of biological aerosol particles and ice nuclei during and after rain. *Atmos. Chem. Phys.*, 13 (13), 6151-6164. https://doi.org/10.5194/acp-13-6151-2013

Jaenicke R., *et al*., 2007. Omnipresence of biological material in the atmosphere. *Environmental Chemistry*, 4 (4), 217-220. https://doi.org/10.1071/EN07021

Jaing C., *et al.*, 2020. Sierra Nevada sweep: Metagenomic measurements of bioaerosols vertically distributed across the troposphere. *Sci. Rep.*, 10 (1), 12399. https://doi.org/10.1038/s41598-020-69188-4

Jones A.M., Harrison R.M., 2004. The effects of meteorological factors on atmospheric bioaerosol concentrations—a review. *Sci. Tot. Environ*, 326 (1), 151-180. https://doi.org/10.1016/j.scitotenv.2003.11.021

Jones S.E., *et al.*, 2008. Potential for atmospheric deposition of bacteria to influence bacterioplankton communities: Atmospheric deposition as immigration events. *FEMS Microbiol. Ecol.*, 64 (3), 388-394. https://doi.org/10.1111/j.1574-6941.2008.00476.x

Joung Y.S., *et al.*, 2017. Bioaerosol generation by raindrops on soil. *Nat. Comm.*, 8 (1), 14668. https://doi.org/10.1038/ncomms14668

Keuschnig C., *et al.*, 2023. Selection processes of Arctic seasonal glacier snowpack bacterial communities. *Microbiome*, 11 (1), 35. https://doi.org/10.1186/s40168-023-01473-6

Kleinteich J., *et al.*, 2017. Pole-to-pole connections: Similarities between arctic and antarctic microbiomes and their vulnerability to environmental change. *Front. Ecol. Evol.*, 5137. https://doi.org/10.3389/fevo.2017.00137

Liu X., Salles J.F., 2024a. Drivers and consequences of microbial community coalescence. *ISME J.*, 18 (1), wrae179. https://doi.org/10.1093/ismejo/wrae179

Liu X., Salles J.F., 2024b. Lose-lose consequences of bacterial community-driven invasions in soil. *Microbiome*, 12 (1), 57. https://doi.org/10.1186/s40168-024-01763-7

Maccario L., *et al.*, 2019. Sources and selection of snow-specific microbial communities in a Greenlandic sea ice snow cover. *Sci. Rep.*, 9 (1), 2290. https://doi.org/10.1038/s41598-019-38744-y

Malard L.A., Pearce D.A., 2022. Bacterial colonisation: From airborne dispersal to integration within the soil community. *Front. Microbiol.*, 13, 782789. https://doi.org/10.3389/fmicb.2022.782789

Malik A.A., *et al.*, 2016. Soil fungal: Bacterial ratios are linked to altered carbon cycling. *Front. Microbiol.*, 7, 01247. https://doi.org/10.3389/fmicb.2016.01247

Mallon C.A., *et al.*, 2018. The impact of failure: Unsuccessful bacterial invasions steer the soil microbial community away from the invader's niche. *ISME J.*, 12 (3), 728-741. https://doi.org/10.1038/s41396-017-0003-y

Martiny J.B.H., *et al.*, 2006. Microbial biogeography: Putting microorganisms on the map. *Nat. Rev. Microbiol.*, 4 (2), 102-112. https://doi.org/10.1038/nrmicro1341

Meier F.C., Lindbergh C.A., 1935. Collecting micro-organisms from the arctic atmosphere: With field notes and material. *Sci. Mon.*, 40 (1), 5-20.

Meola M., *et al.*, 2015. Bacterial composition and survival on sahara dust particles transported to the european Alps. *Front. Microbiol.*, 6:1454. https://doi.org/10.3389/fmicb.2015.01454

Mescioglu E., *et al.*, 2019. Dust-associated airborne microbes affect primary and bacterial production rates, and eukaryotes diversity, in the Northern Red Sea: A mesocosm approach. *Atmosphere*, 10 (7), 358. https://doi.org/10.3390/atmos10070358

Michaud J.M., *et al.*, 2018. Taxon-specific aerosolization of bacteria and viruses in an experimental ocean-atmosphere mesocosm. *Nat. Comm.*, 9 (1), 2017. https://doi.org/10.1038/s41467-018-04409-z

Miller T.E., 1994. Direct and indirect species interactions in an early old-field plant community. *Am. Nat.*, 143 (6), 1007-1025. https://doi.org/10.1086/285646

Miller T.E., *et al.*, 2009. The ghost of competition present. *Am. Nat.*, 173 (3), 347-353. https://doi.org/10.1086/596531

Morris C.E., *et al.*, 2004. Ice nucleation active bacteria and their potential role in precipitation. *Journal de Physique IV (Proceedings)*, 121, 87-103. https://doi.org/10.1051/jp4:2004121004

Na H., *et al.*, 2023. Asian dust-transported bacteria survive in seawater and alter the community structures of coastal bacterioplankton in the Yellow Sea. *Glob. Planet. Change*, 224, 104115. https://doi.org/10.1016/j.gloplacha.2023.104115

Nagler M., *et al.*, 2016. Soil microbial communities along the route of a venturous cycling trip. *Applied Soil Ecology*, 99, 13-18. https://doi.org/10.1016/j.apsoil.2015.11.010

Ng T.W., *et al*., 2017. Importance of stress-response genes to the survival of airborne *Escherichia coli* under different levels of relative humidity. *AMB Express*, 7 (1), 71. https://doi.org/10.1186/s13568-017-0376-3

Ng T.W., *et al*., 2018. Influence of membrane fatty acid composition and fluidity on airborne survival of *Escherichia coli*. *Appl. Microbiol. Biotechnol.*, 102 (7), 3327-3336. https://doi.org/10.1007/s00253-018-8826-7

Nicholson W.L., *et al*., 2005. The solar UV environment and bacterial spore UV resistance: Considerations for Earth-to-Mars transport by natural processes and human spaceflight. *Mutation Research*, 571 (1-2), 249-264. https://doi.org/10.1016/j.mrfmmm.2004.10.012

Nioh I., Furusaka C., 1968. Growth of bacteria in the heat-killed cell suspensions of the same bacteria. *J. Gen. Appl. Microbiol.,* 14 (4), 373-385. https://doi.org/10.2323/jgam.14.373

Park J., *et al*., 2018. Effects of Asian dust events on atmospheric bacterial communities at different distances downwind of the source region. *J. Environ. Sci.*, 72, 133-139. https://doi.org/10.1016/j.jes.2017.12.019

Pasteur L., 1860. Nouvelles expériences relatives aux générations dites spontanées. *Comptes rendus hebdomadaires des séances de l'Académie des sciences, t. 51*, 675-678.

Pearson D.E., *et al*., 2018. Community assembly theory as a framework for biological invasions. *Trends Ecol. Evol.*, 33 (5), 313-325. https://doi.org/10.1016/j.tree.2018.03.002

Peter H., *et al*., 2014. Bacterial diversity and composition during rain events with and without Saharan dust influence reaching a high mountain lake in the Alps. *Environ. Microbiol. Reports*, 6 (6), 618-624. https://doi.org/10.1111/1758-2229.12175

Prospero J.M., *et al*., 2005. Interhemispheric transport of viable fungi and bacteria from Africa to the Caribbean with soil dust. *Aerobiologia*, 21 (1), 1-19. https://doi.org/10.1007/s10453-004-5872-7

Rahav E., *et al*., 2016a. The impact of atmospheric dry deposition associated microbes on the south-eastern Mediterranean Sea surface water following an intense dust storm. *Front. Mar. Sci.*, 3, 127. https://doi.org/10.3389/fmars.2016.00127

Rahav E., *et al*., 2016b. Evaluating the impact of atmospheric depositions on springtime dinitrogen fixation in the Cretan Sea (Eastern Mediterranean)—A mesocosm approach. *Front. Mar. Sci.*, 3, 180. https://doi.org/10.3389/fmars.2016.00180

Reche I., *et al*., 2018. Deposition rates of viruses and bacteria above the atmospheric boundary layer. *ISME J.*, 12 (4), 1154-1162. https://doi.org/10.1038/s41396-017-0042-4

Rillig M.C., *et al*., 2015. Interchange of entire communities: Microbial community coalescence. *Trends Ecol. Evol.*, 30 (8), 470-476. https://doi.org/10.1016/j.tree.2015.06.004

Rodó X., *et al*., 2024. Microbial richness and air chemistry in aerosols above the PBL confirm 2,000-km long-distance transport of potential human pathogens. *Proc. Natl Acad. Sci. USA*, 121 (38), e2404191121. https://doi.org/10.1073/pnas.2404191121

Roeters S.J., *et al*., 2021. Ice-nucleating proteins are activated by low temperatures to control the structure of interfacial water. *Nat. Comm.*, 12 (1), 1183. https://doi.org/10.1038/s41467-021-21349-3

Sahyoun M., *et al*., 2017. Impact of bacterial ice nucleating particles on weather predicted by a numerical weather prediction model. *Atmos. Environ.*, 170, 33-44. https://doi.org/10.1016/j.atmosenv.2017.09.029

Smakman F., Hall A.R., 2022. Exposure to lysed bacteria can promote or inhibit growth of neighboring live bacteria depending on local abiotic conditions. *FEMS Microbiol. Ecol.*, 98 (2), fiac011. https://doi.org/10.1093/femsec/fiac011

Smith B.L., King M.D., 2023. Quiescence of *Escherichia coli* aerosols to survive mechanical stress during high-velocity collection. *Microorganisms*, 11 (3), 647. https://doi.org/10.3390/microorganisms11030647

Steinhaus E.A., Birkeland J.M., 1939. Studies on the life and death of bacteria: I. The senescent phase in aging cultures and the probable mechanisms involved. *J. Bacteriol.*, 38, 249-261. https://doi.org/10.1128/jb.38.3.249-261.1939

Stroeve J., *et al*., 2007. Arctic sea ice decline: Faster than forecast. *Geophys. Res. Lett.*, 34, L09501. https://doi.org/10.1029/2007GL029703

Tanaka D., *et al*., 2019. Airborne microbial communities at high-altitude and suburban sites in Toyama, Japan suggest a new perspective for bioprospecting. *Front. Bioeng. Biotechnol.*, 712. https://doi.org/10.3389/fbioe.2019.00012

Tesson S.V.M., Šantl-Temkiv T., 2018. Ice nucleation activity and aeolian dispersal success in airborne and aquatic microalgae. *Front. Microbiol.*, 9, 2681. https://doi.org/10.3389/fmicb.2018.02681

Thakur M.P., *et al*., 2019. Microbial invasions in terrestrial ecosystems. *Nat. Rev. Microbiol.*, 17 (10), 621-631. https://doi.org/10.1038/s41579-019-0236-z

Thomas R.J., 2013. Particle size and pathogenicity in the respiratory tract. *Virulence*, 4 (8), 847-858. https://doi.org/10.4161/viru.27172

Tignat-Perrier R., *et al*., 2020a. Seasonal shift in airborne microbial communities. *Sci. Tot. Environ*, 716, 137129. https://doi.org/10.1016/j.scitotenv.2020.137129

Tignat-Perrier R., *et al*., 2020b. Microbial ecology of the planetary boundary layer. *Atmosphere*, 11 (12), 1296. https://doi.org/10.3390/atmos11121296

Van Leeuwenhoek A., 1677. Observations, communicated to the publisher by Mr. Antony van Leewenhoeck, in a dutch letter of the 9th Octob. 1676. here English'd: concerning little animals by him observed in rain-well-sea- and snow water; as also in water wherein pepper had lain infused. *Philos. Trans. R. Soc.,* 12 (133), 821-831. https://doi.org/10.1098/rstl.1677.0003

Walters K.E., *et al*., 2022. Routes and rates of bacterial dispersal impact surface soil microbiome composition and functioning. *ISME J.*, 16 (10), 2295-2304. https://doi.org/10.1038/s41396-022-01269-w

Weil T., *et al*., 2017. Legal immigrants: Invasion of alien microbial communities during winter occurring desert dust storms. *Microbiome*, 5 (1), 32. https://doi.org/10.1186/s40168-017-0249-7

Wilson T.W., *et al*., 2015. A marine biogenic source of atmospheric ice-nucleating particles. *Nature*, 525 (7568), 234-238. https://doi.org/10.1038/nature14986

Womack A.M., *et al*., 2010. Biodiversity and biogeography of the atmosphere. *Philos. Trans. R. Soc. B Biol. Sci.*, 365 (1558), 3645-3653. https://doi.org/10.1098/rstb.2010.0283

Womack A.M., *et al*., 2015. Characterization of active and total fungal communities in the atmosphere over the Amazon rainforest. *Biogeosciences*, 12 (21), 6337-6349. https://doi.org/10.5194/bg-12-6337-2015

Xing J., *et al*., 2021. The legacy of bacterial invasions on soil native communistes. *Environ. Microbiol.*, 23 (2), 669-681. https://doi.org/10.1111/1462-2920.15086

Yafetto L., *et al*., 2008. The fastest flights in nature: High-speed spore discharge mechanisms among fungi. *PLoS ONE*, 3 (9), e3237. https://doi.org/10.1371/journal.pone.0003237

Zhen H., *et al*., 2013. Release of free DNA by membrane-impaired bacterial aerosols due to aerosolization and air sampling. *Appl. Environ. Microbiol.*, 79 (24), 7780-7789. https://doi.org/10.1128/AEM.02859-13

Zhen Q., *et al*., 2017. Meteorological factors had more impact on airborne bacterial communities than air pollutants. *Sci. Tot. Environ*, 601-602, 703-712. https://doi.org/10.1016/j.scitotenv.2017.05.049

Zhou S.-Y.-D., *et al*., 2021. Microbial flow within an air-phyllosphere-soil continuum. *Front. Microbiol.*, 11, 615481. https://doi.org/10.3389/fmicb.2020.615481

Zweifel U.L., *et al*., 2012. High bacterial 16S rRNA gene diversity above the atmospheric boundary layer. *Aerobiologia*, 28 (4), 481-498. https://doi.org/10.1007/s10453-012-9250-6

Chapter 13

Biology of the air we breathe: Potential impact on human health

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As illustrated in the previous chapters, microorganisms can be found in the upper levels of the stratosphere right down to the very air we breathe. This microbiome includes a variety of bacteria, fungi, viruses, and importantly their associated genetic material. Additionally, there is an enormous array of microscopic particles derived from plants and animals that can be allergenic to humans. All these biologics can have impacts on our health. These bioaerosols are prolific with numbers being in the millions per cubic metre of the air we might breathe, contributing to more than 10% of PM_{10} (see Chapter 2 for definitions). They have wide ranges in size, from nanometre to fractions of a millimetre.

In the first part of this chapter, we present the natural and man-made origins of these aerosols, and how they proliferate across the globe as well as locally in the air we respire. In the second part, a brief outline of the way we breathe and consequently the intake of aerosols into respiratory tract is presented. The deposition mechanism within the different areas of the tract is reviewed, considering the particulate size, where deposition is more likely to take place and subsequently how they are transferred across into the bloodstream. This is important considering the infection aspect, were the intrusion of bioaerosols beyond the respiratory tract might lead to the development of disease. In the third part we present a brief overview of the various methods of counting or measuring bioaerosols that leads to assessment of the the likelihood that we might inhale them. Methods of bioaerosol sampling have vastly improved over recent years, especially considering DNA techniques, etc., but fundamentally they focus on capturing, counting and sizing aerosols. Finally, in the last part some familiar viral, bacterial, fungal, protist and allergenic bioaerosols are described along with how they are inhaled and cross into the bloodstream, and cause infection and disease. A comment on emerging gaps and uncertainty concludes this review.

⏩ Biological particles in the air

Bioaerosols generated by human activities, particularly those containing pathogenic or allergenic microorganisms, pose significant risks to human health due to their potential to cause disease and allergic reactions. Human activity has a strong influence on

localised bioaerosols. Indoor environments contain particles of skin and contribution from respiratory activity. This is especially the case when someone is shedding when ill, as well as contributions from pets (Fagade *et al*., 2023). The presence of farms and high densities of animals, landfills, wastewater treatment plants and waste management activities (e.g., composting) can significantly influence microbial communities (Xie *et al.*, 2021). Sources from any particular human-activity are not often easy to delineate, as there are limited marker compounds to distinguish them. However, composting might have higher *Aspergillus* species and wastewater enteric bacteria as indicators. Some typical examples are presented below.

Pollution "haze" events, the suspension of fine particles that reduce visibility (Wei *et al.*, 2020), particularly in Asia, drive changes to bioaerosol components. Highest microbial activity can be found in moderate pollution events (Hu *et al.*, 2020). An increase in fine particles during haze events and increase in coarser fraction during foggy days presents slightly different patterns of bacteria and fungi. Microbial structure varies between particle size fractions. Higher levels of allergic, pathogenic and infectious species are observed during haze events, whilst increased bioaerosol numbers have also been observed during biomass burning, leading to increases in viable bacterial and fungal spores at the fire front which releases and generates high concentration of aerosols as described in detail in Chapter 8.

Bioaerosol pollution can be localised, both in urban and rural areas. Within the urban environment, traffic and building architecture can lead to stagnation of pollution within street canyons, with the build-up of particulates and gases close to the ground

Table 13.1. Examples of bioaerosol loading in indoor and outdoor urban/rural environments.

Location/context	Example aerosol loading	Reference
Indoor: Research institute facilities, Seoul, Republic of Korea	Bacterial bioaerosol concentrations were 170, 94, and 77 CFU/m^3, the average fungal bioaerosol concentration was 205 CFU/m^3 in a canteen and <51 CFU/m^3 at all other sampling locations	Jeong *et al.*, 2022
Indoor: Middle school cafeteria in Illinois, USA	Fungal bioaerosol concentration of 460 CFU/m^3, and the indoor/outdoor ratio was approximately 1.18	Scheff *et al.*, 2000
Indoor: School cafeteria, Poland	Fungal bioaerosol concentrations of 27–310 CFU/m^3	Małecka-Adamowicz *et al.*, 2020
Urban/Rural, Beijing, China	2,799 CFUs/m^3 in a trafficked/urban area compared to 1,484 CFU/m^3 in a greener area	Fang *et al.*, 2007
Urban/Rural, Marseille, France	791 CFU/m^3 bacteria in urban Marseille compared to 42 CFU/m^3 in a nature reserve on an offshore island	di Giorgio *et al.*, 1996
Urban/Rural, indoor/outdoor, Guangzhou, Southern China	Higher in urban areas (955 ± 259 CFU/m^3) compared to suburban areas (850 ± 85 CFU/m^3), the highest indoor concentrations in the market (2,170 ± 798 CFU/m^3) and gymnasium (2,010 ± 300 CFU/m^3)	Ni *et al.*, 2024

CFU, colony forming unit.

and the buildings (Xie *et al.,* 2003; Karra *et al.,* 2011; Yazid *et al.,* 2014). Unpublished research has shown that biological particles could also build-up in such a way, with significantly more microbes (50%) at 0.8 m than at 1.68 m height above the pavement in a street canyon in Glasgow, UK (D. Sykes, unpublised data). Many studies have compared indoor against outdoor locations across a range of urban and rural environments. Bioaerosols can contribute between 5 and 34% of indoor air pollution. In rural sites, some activities such as composting can generate significant concentration or numbers of bacteria and fungi, but there is little evidence for occupational and near neighbour impact. Within 250 or 500 m of sites dilution leads to background bioaerosol levels, and few studies have seen rises in health problems associated with biological particles (Robertson *et al*., 2019). Table 13.1 presents examples of typical bioaerosol loadings in indoor/outdoor environments and from urban/rural settings.

⏩ The science of lungs and breathing

How we breathe

We inhale and exhale air, and its constituent gases and any aerosols it contains, at approximately 8 to 10 litres per minute, or an approximate breathing flow rate (Q) of 0.14 to 0.18 l/s (as illustrated in Figure 13.1), where we take a full breath about every 3 seconds (Stettler *et al.*, 2022). Daily, this translates to between 8 and 24 m^3 of air depending on whether we are completely at rest or moderately active, respectively (Pleil *et al.*, 2021).

Oxygen from the air must penetrate to the furthest reaches of the lungs to cross into the bloodstream. For this to happen the muscles of the diaphragm and the rib cage contract, causing an expansion of the lungs, which have a reduced pressure compared to the air outside of the body. This allows air to be drawn right from the upper reaches of the respiratory tract to the alveolar sacs. Aerosols will also be drawn into the respiratory tract and the depth of penetration, and their deposition within the lungs, are largely dependent upon particle size based on the same principles of physics described in Chapter 2.

Aerosol deposition in the body

The risk of a bioaerosol to a human depends on its capacity to penetrate and deposit in the respiratory tract. These capacities are defined by the size and shape of the inhaled aerosols –which confer their aerodynamic size. Bioaerosols range in size from 0.01 to 100 μm, all of which are readily inhalable (Whitby *et al.*, 2022). Their capacity for deposition within the respiratory tract has been defined by the Comité Européen de Normalisation[8] following three conventions: i) the inhalable fraction (i.e., the mass fraction of total airborne particles which is inhaled through the nose and mouth) ii) the thoracic fraction (the mass fraction of inhaled particles penetrating beyond the larynx) and iii) the respirable fraction (the mass fraction of inhaled particles penetrating to the unciliated airway) (Figure 13.1). The regions of deposition and aerosol penetration within the upper body, once breathed into the lungs, are illustrated in Figure 13.2.

8. Comité Européen de Normalisation., 1993. Workplace atmospheres. Size fraction definitions for measurement of airborne particles. https://knowledge.bsigroup.com/products/workplace-atmospheres-size-fraction-definitions-for-measurement-of-airborne-particles?version=standard.

Wang *et al.* (2022) documented the penetration and sub-micron deposition of ultra-fine particles (UFPs, those smaller than 0.1 μm). They noted that these finer particles tend to deposit in the alveolar regions and are more likely to penetrate the air-blood barrier. Furthermore, Morawska *et al.* (2022) observed that particles smaller than 50 nm exhibit deposition fractions exceeding 50%, whereas particles between 100 nm and 1 μm show minimal deposition (10–30%, depending on the type of particle).

The dose received by an individual due to bioaerosol deposition is dependent upon several physicochemical properties. These include bioaerosol concentration, exposure to the aerosol, cellular exposure and the consequential transport and deposition area within the respiratory tract (Wu *et al.*, 2018).

Though many bioaerosols deposit in the upper airways of the respiratory tract within the epithelium, some will penetrate beyond the epithelium into the bloodstream and will sequentially end up within the organs of the body (Morawska *et al.*, 2022; Wang *et al.*, 2022). Particles in the $PM_{2.5}$ range are mostly intercepted at the air-blood barrier, whereas UFPs are thought to be able to cross more easily into the bloodstream. Similarly, the blood-brain barrier and blood-placental barrier are thought to be very difficult to penetrate for $PM_{2.5}$ but UFPs are more likely to cross these barriers, though such research seems rather limited to date (Wang *et al.*, 2022). The epithelium within the throat, for example, is a thick, protective multi-cellular layer which provides a barrier to larger particles. This is in contrast to the air-blood barrier (or other barriers discussed) of the alveoli which is a two-cell layer enabling the easy passage of gases (O_2 and CO_2) and hence UFPs (Bustos *et al.*, 2023).

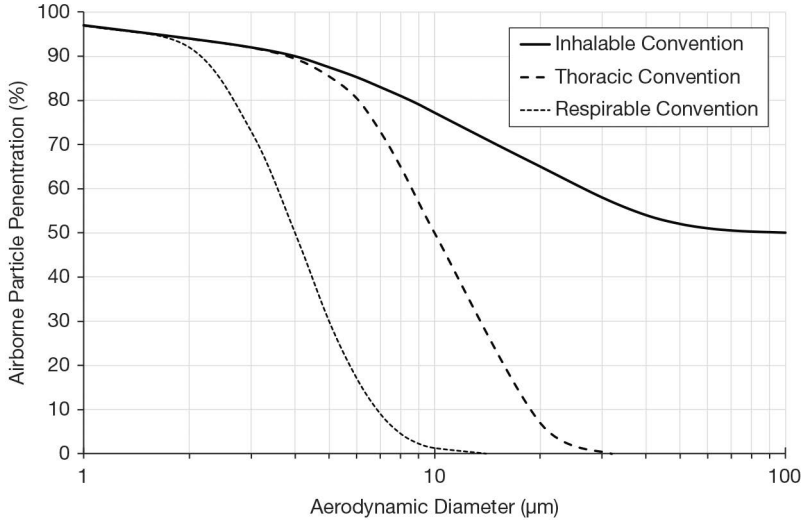

Figure 13.1. Conventions showing percentage of airborne particles penetrating the respiratory tract as a part of total airborne particles (after Comité Européen de Normalisation[8]).

Excessive exposure to aerosols is a problem faced globally, with billions of people breathing air that exceeds current World Health Organization (WHO, 2022) standards for healthy air. This has led to what the WHO describes as a global crisis with an estimated 6.7 million premature deaths as the result of air pollution in 2019. According to

the WHO, these deaths are primarily "noncommunicable diseases (NCDs), including ischemic heart disease, stroke, lung cancer, asthma, chronic obstructive pulmonary disease (COPD), and diabetes" (WHO, 2024), many due to diseases in the body beyond the lungs, that are a consequence of penetration of particulates into the bloodstream. Overall, air pollution and particulates are believed to cause more than 100 million disability-adjusted life years as well as increased risks of death (Wang *et al.*, 2022).

With increased loading of bioaerosols, more immediate or drastic consequences compared with other aerosols or particulate matter potentially exist. This is especially true when considering pathogens, such as viruses, bacteria, or fungal spores, that might cause ailments from the common cold, flu, Aspergillosis and more serious diseases like tuberculosis, COVID-19, or Legionnaires' disease.

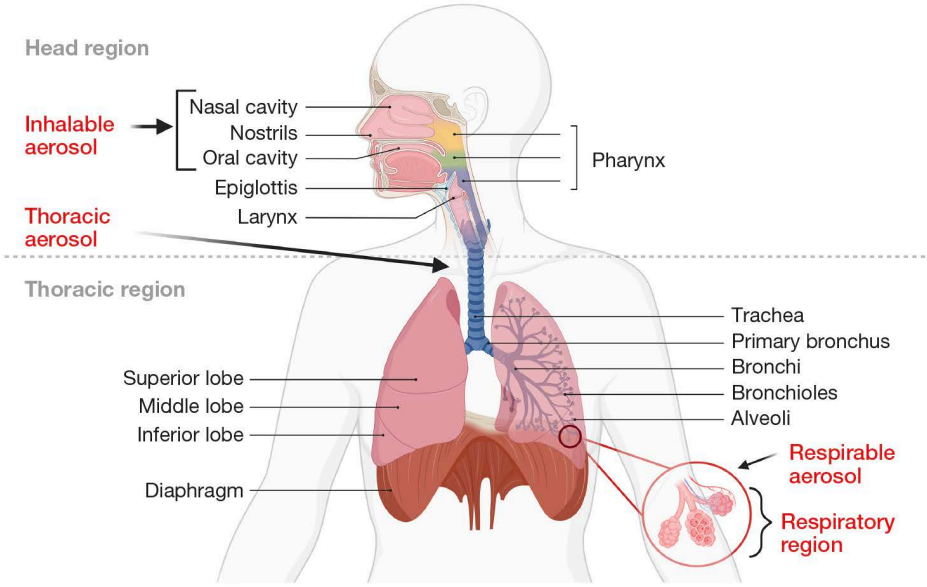

Figure 13.2. Regions of deposition and aerosol penetration within the upper body (after Khan, 2013).

The science of sampling bioaerosols

To understand the number, size, type and distribution of bioaerosols in the air and the part that we might breathe, the science of sampling or measurement of bioaerosol has evolved considerably. The origin of the science lies in the mid-19th century when aerosols were first sampled using impactors to study the relationship between dust and disease (Marple, 2004).

Bioaerosols are usually captured by one of the following means filtration, impaction, impingement, and electrostatic precipitation, or by combining these technologies (Mainelis, 2020). Often a collection medium is involved (especially when searching for microorganisms) enabling the culturing or stabilising of the bioaerosol. This is unique with biological particles as aspiration, transport, and deposition may result in a loss of integrity caused by the sampling process. Bioaerosol sampling might be

considered less precise than aerosol sampling (or other sampling techniques), as it cannot be guaranteed that every microbe, spore or enzyme can be counted or sampled (Sykes, 2005), due to the loss of integrity, or inhibited culture of the microorganisms or bioaerosol being counted. Some of these difficulties are also discussed in Chapter 3.

Filtration is the capture of particles onto or within the fibres of a filter prior to elution or counting. It is the most simplistic method, allowing for long sampling times, but introduces the possibility of damage to the bioaerosols and requires post-processing time. However, it has the advantage of being able to capture a multitude of different bioaerosols at the same time, at high concentrations, although it can only provide a time-weighted average. Impaction is the capture of particles from the airstream using inertia via the impaction onto a surface or plate. It is a quick and precise technique which can capture microorganisms onto agar plates, often eliminating losses from desiccation associated with filtration. Typically, Andersen samplers (single or multiple-stage viable count impactors, described in Chapter 2) are used for microbial counts. A similar method of impaction is used for spore traps, deployed primarily for fungi and pollen. Both spore traps and Andersen samplers suffer from limited sampling times as they can quickly become overloaded with samples. Impingement is the capture of particles from the airstream using inertia into a liquid. The advantage of impingement is in maintaining viability of microbes and longer sampling times than filtration times, however it can be subject to missing smaller particle sizes and not having a high sampling rate. Impingement can also be used to collect viruses and other bioaerosols (Mainelis, 2020; Sykes, 2005).

The counting (measurement) of microbes that have been sampled is a time consuming, but relatively simple process, using either spread plating or by depending on direct impaction on agar plates. Other methods of counting of bioaerosols include spore counts, non-viable methods using dyes or DNA based counts for microbes, viral PCR counts, and even spectrophotometric techniques (Kumar and Ghosh, 2019).

The use of Next Generation Sequencing (NGS), a DNA-based method, allows for the direct identification or characterization of a much larger number of individuals and can give broader information about microbial diversity than what can be attained with culture-based methods. Such techniques can enable sampling from surfaces, soil samples, or from air samplers at high flow rates, e.g. up to 1,000 l/min (Núñez *et al.*, 2016), which is typically much higher than other counting methods such the Andersen sampler at 28.3 l/min because there is not a concern about protection viability.

Meanwhile the fluorescent property of various biomolecules can be used to distinguish an aerosol with biological origin (Huffman *et al.*, 2020). Thus laser-(or light)-induced fluorescence (LIF) for bio-particulate matter identification and quantification allow for improved bio-particulate matter exposure assessment beyond what can be achieved with traditional culture-based methods, and used in real-time, when compared to many of the above techniques (Wu *et al.*, 2018).

⏩ Diseases associated with lung biology

"Bad air" has long been associated with the potential spread of disease. Miasma theory was the belief that secretions from decaying carcasses, rotting vegetables, mold or dust particles were the cause of diseases such as cholera, malaria, and the bubonic plague

(Kannadan, 2018). Louis Pasteur is well known for demonstrating that air contained living organisms that were the cause of fermentations (Fleming, 1947; Smith, 2012). Since Pasteur's discovery, investigations into the cause of diseases from "bad air" have been shown to be associated with myriads of biological contaminants including viruses, bacteria, fungi and other biological particles such as pollen.

Overview of lung diseases

Illnesses and diseases caused through airborne transmission routes including coughing, sneezing and aerosols, can occur from many biological particles. Viruses that are ubiquitous globally can result in respiratory illnesses and diseases and are caused by Rhinoviruses (RV), Influenza viruses and Coronaviruses (CoV), among others. RV, are often the cause of seasonal common colds that can cause both mild symptoms in the form upper respiratory tract infections and more severe lower respiratory tract infections that can cause hospitalisation (Esneau *et al.*, 2022; Ljubin-Sternak and Meštrović, 2023). CoV are a family of respiratory viruses that were first identified in the 1960s and typically cause mild respiratory infections within both humans and animals. Like some RV, CoV can result in serious illnesses such as severe acute respiratory syndrome (SARS) or Middle East respiratory syndrome[9] (MERS). These types of CoV are believed to originate from animals but evolve or mutate to different hosts, such as humans. Meanwhile influenza is thought to affect 10% of the world annually, and can during pandemics have a high mortality rate, with deaths in the pandemic of 1918 killing more than 10 million people (Javanian *et al.*, 2021). Bacteria such as *Mycobacterium tuberculosis* spp. and *Legionella pheumophilia* are also crucially important pathogens of the respiratory system as described in detail below.

The respiratory microbiome is crucial in influencing the human response to inhaled bioaerosols, which act as pollutants or irritants to the lungs. The microbiome's interaction with inhaled irritants can affect susceptibility to respiratory infections, potentially exacerbating lung diseases (Adar *et al.*, 2016). Exposure to airborne particles can induce oxidative stress, inflammation, and immune responses, leading to acute and chronic respiratory effects (Kelly and Fussell, 2020). These effects can disrupt the microbiome balance, influencing the persistence and exacerbation of bacterial pathogens (Adar *et al.*, 2016; Kelly and Fussell, 2020). Understanding the interplay between biological contaminants, pollutants, and the respiratory microbiome is essential for a holistic view of respiratory health.

Bacterial tolerance and persistence in the respiratory environment can complicate the treatment of respiratory diseases. Bacteria can develop persistence mechanisms in the respiratory tract, such as biofilm formation and phenotypic changes, making them resistant to host defences and antimicrobial treatments (Trastoy *et al.*, 2018). These persistence mechanisms contribute to chronic respiratory infections and complicate treatment efforts. The respiratory microbiome plays a role in these persistence mechanisms, providing a favorable environment for bacteria to evade immune responses and resist treatment (Adar *et al.*, 2016; Trastoy *et al.*, 2018).

9. European Centre for Disease Prevention and Control. Coronaviruses. Retrieved October 8, 2024, from https://www.ecdc.europa.eu/en/coronaviruses.

Viral diseases: COVID and influenza

Acute respiratory diseases caused by viruses are among the most common worldwide (Barbuti *et al.*, 2002). The COVID-19 pandemic and the annual flu epidemic are two of the most studied respiratory diseases of viral origin. Both have significant impacts on public health, causing widespread illness and death, particularly among vulnerable populations (Gomez *et al.*, 2021; Singer, 2020).

Viruses can enter the respiratory system by inhaling virus-laden droplets and aerosols. These airborne particles are expelled from infected individuals during coughing, sneezing, talking, or even normal breathing, contributing significantly to the transmission of respiratory viruses like SARS-CoV-2 and influenza (de Gabory *et al.*, 2020; Scheuch, 2020).

Droplets and aerosols are the two main types of particles responsible for the airborne transmission of respiratory viruses. Droplets are typically larger than 5 μm, follow ballistic trajectories, and are more likely to settle, dropping out of the air onto surfaces. They are produced during activities like coughing, sneezing, or talking and generally infect individuals in close proximity (de Gabory *et al.*, 2020; Wang *et al.*, 2021). Larger droplets however, upon exhalation from an infected patient, can quickly dehydrate, causing their decrease in size; from larger particles, or droplets (>10 μm) to smaller particles. This has a significant influence on long-range transmission of the aerosol (Stettler *et al.*, 2022).

In contrast, particles that are smaller than 5 μm can remain suspended in the air for extended periods, travelling longer distances. These particles are produced during regular breathing and other expiratory activities, making them more versatile in their capacity to infect individuals both near and far from the source (Scheuch, 2020; Wang *et al.*, 2021). These smaller particles typically contain more viral particles, such as SARS-CoV-2 or influenza virions. The viruses are not directly inhaled but are generally inhaled as part of the fluids (such as mucous) from the diseased patient. It is estimated that 85% of viral load (RNA copies) is contained within the fine fraction (less than or equal to 5 μm) of the mucous (Stettler *et al.*, 2022).

Upon inhalation, the size of the virus-laden mucous particle determines their deposition in the respiratory tract. Larger droplets generally settle in the upper airways, while smaller aerosols can penetrate deeper, reaching the lower respiratory tract, including the alveoli (Wang *et al.*, 2021). Specifically, viruses like influenza-A primarily infect the nasal respiratory epithelium, contributing to their effective airborne transmission (Richard *et al.*, 2020).

SARS-CoV-2 enters host cells by binding its spike (S) protein to the ACE2 receptor –a critical step for viral entry (Jackson *et al.*, 2022; Yesudhas *et al.*, 2021). The immune response to infection varies considerably and influences disease severity. In some patients, particularly the elderly, an overactive immune response (a cytokine storm) can trigger systemic inflammation, acute respiratory distress syndrome and multiple organ failure (Meftahi *et al.*, 2020; Tian *et al.*, 2020). In contrast, early infection may be marked by immune suppression, while severe cases can involve complications such as immunothrombosis, where clot formation further impairs organ function (Bonaventura *et al.*, 2021). Although the host immune response is crucial in determining the outcome of SARS-CoV-2 infection, the environmental conditions affecting

the dispersal of viral particles also play an important role in transmission dynamics. Recent studies have examined how factors such as temperature, humidity, airflow and UV radiation impact the airborne movement and viability of the virus.

Temperature is a key factor in viral viability within aerosols. For example, higher temperatures (above 25°C) have been linked to a moderate reduction in virus transmission, although this effect alone is insufficient to prevent spread (da Silva *et al.*, 2021; Xu *et al.*, 2021). Experimental work indicates that at 40°C, a 90% reduction in infectious virus can occur within 4.8 minutes under high intensity simulated sunlight (Dabisch *et al.*, 2021). Nonetheless, the overall impact of temperature is complex, with both positive and negative correlations observed; thus, temperature control on its own is not a reliable strategy for reducing exposure (Foat *et al.*, 2022). Humidity also affects the airborne movement and viability of viral particles. Higher relative humidity levels (61–80%) have been shown to significantly reduce SARS-CoV-2 viability, whereas lower humidity may favor virus survival by promoting salt crystallisation in aerosol droplets, leading to a rapid loss of infectivity (Deeb *et al.*, 2023; Löndahl and Alsved, 2022; Mao *et al.*, 2022). Moreover, the interplay between humidity and factors such as spreading time further complicates its overall impact on transmission (Mao *et al.*, 2022). Ventilation is crucial for mitigating airborne transmission. Mechanically ventilated environments can alter the dispersal of viral particles, with airflow velocity affecting the trajectories of respiratory droplets and aerosols (Deeb *et al.*, 2023). Furthermore, the proper use of heating, ventilation, and air conditioning (HVAC) systems may help maintain pathogen filtration and reduce transmission risk, although proximity to an infected individual can counteract these benefits (Foat *et al.*, 2022). UV radiation has been demonstrated to inactivate viruses in aerosols. An increased UV dose is associated with a reduction in the survival fraction of viruses, with both animal and human studies linking UV exposure to decreased transmission (Thornton *et al.*, 2022). In fact, simulated sunlight, which incorporates UV radiation, appears to have a more pronounced effect on the decay of infectious SARS-CoV-2 than humidity across a range of conditions (Dabisch *et al.*, 2021). In a similar way to SARS-CoV-2, influenza viruses are a major cause of respiratory infections, resulting in seasonal epidemics and occasional pandemics. These viruses mainly infect cells in the upper airways by attaching to receptors using a protein called hemagglutinin. Once inside, the virus uses the cell's own machinery to reproduce and spread to nearby cells (Javanian *et al.*, 2021; Mifsud *et al.*, 2021; Peteranderl *et al.*, 2016). The immune defences work in two stages. First, a rapid, non-specific response tries to limit the infection. Later, specialised immune cells target and eliminate the virus. However, if this response becomes too strong, it can lead to a dangerous overreaction known as a cytokine storm, which may cause severe tissue damage and worsen the illness (Iwasaki and Pillai, 2014; Frank and Paust, 2020). Regular updates to influenza vaccines are necessary because the virus continually changes over time (Kreijtz *et al.*, 2011).

Beyond immune responses, the environment plays a crucial role in the spread of influenza viruses. Various conditions, including ambient temperature, relative humidity, ventilation and natural sunlight, affect how long the virus remains viable in the air and its potential to infect others. Temperature is a key factor. Cold conditions, for example, around 5°C, can enhance viral transmission by prolonging the period during which infected hosts shed the virus (Lowen *et al.*, 2007). In temperate regions, winter's low temperatures are linked to increased influenza activity (Peci *et al.*, 2019; Sooryanarain

and Elankumaran, 2015) and generally support a longer survival of the virus in the air (Hemmes *et al.*, 1960). Humidity also influences virus spread. Low relative humidity, common in winter indoor settings, helps the virus remain active by slowing its inactivation and maintaining higher levels of infectious particles (Marr *et al.*, 2019; Yang and Marr, 2011). Conversely, higher humidity can speed up viral inactivation, reducing the number of airborne viruses. The combination of low temperature and low humidity is thought to significantly contribute to influenza epidemics (Yin *et al.*, 2023). Ventilation further affects the dispersal of virus-containing droplets. Good ventilation can remove these droplets from indoor spaces and lower the risk of infection, while poor ventilation allows them to build up, especially under dry conditions (Robey and Fierce, 2022; Yang and Marr, 2011). Although less extensively studied, UV radiation from natural sunlight is known to inactivate influenza viruses, thereby reducing their viability, particularly in outdoor environments.

Both acute respiratory diseases discussed represent an ongoing threat to global health, largely due to the complexities of the immune response they provoke. These infections demonstrate how a well-balanced immune response is essential to successfully contrast the virus while avoiding harmful consequences of over-activity, such as a cytokine storm. Continued research is crucial for developing effective vaccines and therapeutic strategies to improve patient outcomes and control the spread of these highly contagious respiratory viral pathogens.

Bacteria: Tuberculosis and Legionnaires' disease

Bacteria can enter the respiratory tract through both aspiration and inhalation. Aspiration occurs when contaminated secretions from the oropharynx or stomach are aspirated into the lower airways. This is particularly relevant in cases like ventilator-associated pneumonia (VAP), where pathogens are aspirated due to mechanical reflux and contamination (Estes and Meduri, 1995). In inhalation, airborne bacteria are inhaled during normal breathing. These microbes pass through the nasal passages, bypassing the upper respiratory tract's mucociliary defences and ultimately reaching the lower respiratory airways (Martin, 2000). Once bacteria enter the lower respiratory tract, the mucociliary system and alveolar macrophages play crucial roles in recognising and attempting to clear these pathogens, thereby preventing pulmonary infections (Martin, 2000). However, when these defence mechanisms are compromised or overwhelmed, pathogenic bacteria can successfully colonise and infect the lower airways, leading to respiratory diseases.

Among the bacterial pathogens capable of infecting the respiratory tract, *Mycobacterium tuberculosis* and *Legionella pneumophila* are two relevant examples. *M. tuberculosis* is the cause of tuberculosis (TB), an infectious disease that is transmitted through airborne droplets from infected persons who cough or sneeze (Olatunji and Olaboye, 2024). TB has a high mortality and morbidity rates worldwide as it not only infects the respiratory system but can also affect the brain and kidneys (Pai *et al.*, 2016; Rahlwes *et al.*, 2023). The bacillus *M. tuberculosis* primarily affects the lungs but can also impact other parts of the body (Barbuti *et al.*, 2002). TB is transmitted through the air when people with active TB in their lungs cough, spit, speak, or sneeze. The bacillus penetrates the airways and localises in the pulmonary lobes, reaching the broncho-alveolar ramifications (Barbuti *et al.*, 2002).

This area is accessed by evading both mechanical barriers, such as mucus and cilia, and the immune system cells, such as the macrophages. *M. tuberculosis* primarily targets macrophages, and once inside, it inhibits apoptosis, allowing the bacteria to survive and replicate. (Flynn and Chan, 2001; Zhai *et al.*, 2019). The bacterium also prevents the maturation and acidification of phagolysosomes, cellular structures that typically digest pathogens, thereby evading destruction (Dey and Bishai, 2014; Flynn and Chan, 2001; Zhai *et al.*, 2019). This process represents the primary infection, where a mixture of lymphocytes and infected macrophages form a granuloma (Kaplan *et al.*, 2003), which within a period of two months, leads to the necrosis of the surrounding tissues (Dutta and Karakousis, 2014). In most cases, the patients heal once the immune system inactivates the remaining bacilli. However, the primary infection can persist and lead to the infection of other organs and tissues, which will resolve once again with the formation of necrotic tissue. These strategies are collectively adopted by *M. tuberculosis* to persist within the host and cause long-term infections.

Legionella pneumophila is common in water systems that are not effectively maintained whereby pipes that are infrequently used, or where stagnant water exist within systems such as cooling towers, shower heads, taps, hot tubs as well as nebulisers and other respiratory devices (Clopper *et al.*, 2021; Cunha *et al.*, 2016). When emitted as aerosols water droplets, as mists or as vapors, *L. pneumophila* can cause Legionnaires' disease, a severe form of pneumonia, and symptoms include fever, coughing, shortness of breath and aching muscles.

Like *M. tuberculosis, L. pneumophila* is another bacterium able to evade the immune system and replicate in the alveolar macrophages. It primarily infects alveolar macrophages and epithelial cells by avoiding phagolysosome fusion and creating a replication-permissive compartment known as the Legionella-containing vacuole (LCV). This vacuole exhibits endoplasmic reticulum (ER) characteristics, allowing the bacteria to replicate within a protected environment (Iliadi *et al.*, 2022; Newton *et al.*, 2010; Swanson and Hammer, 2000). *L. pneumophila* infection triggers an immune response from the host, mainly through the innate immune system. Lastly, this detects *L. pneumophila* through pattern recognition receptors such as NOD-like receptors and Toll-like receptors. These receptors activate signalling pathways leading to the production of proinflammatory cytokines and interferons, which are crucial for controlling the infection (Liu and Shin, 2019; Naujoks *et al.*, 2018). Macrophages employ several intrinsic resistance mechanisms to combat *L. pneumophila* infection, including inflammasome activation, TNFα (Tumor Necrosis Factor α) production, and interferon responses, in an attempt to limit both bacterial replication and promote the death of the infected cells (Naujoks *et al.*, 2018). Nonetheless, *L. pneumophila* deploys virulence factors such as the Type IV Secretion System to manipulate various host cellular processes, including vesicle trafficking, immune signalling, and mitochondrial dynamics, thereby facilitating bacterial replication and survival (Chauhan and Shames, 2021; Finsel and Hilbi, 2015; Liu and Shin, 2019).

Understanding the biology of respiratory bacterial pathogens like *M. tuberculosis* and *L. pneumophila* is essential for appreciating the complex interactions between inhaled microbes and lung biology. These two pathogens exemplify how the respiratory system, constantly exposed to airborne threats, must employ specific defence

mechanisms that can sometimes be circumvented by determined bacterial strategies. This highlights the need for innovative research to develop effective therapies against such complicated lung infections.

Fungi: Aspergillosis

Aspergillus is a common fungus responsible for aspergillosis. Humans and animals regularly inhale its spores, which are light enough to reach deep into the lungs and pose a particular risk to those with weakened immune systems (Bozza *et al.*, 2002; Latgé, 1999; Vonberg and Gastmeier, 2006). In individuals with strong defences, inhaled spores are usually cleared without causing serious illness, though mild effects such as allergic sinusitis or bronchitis may occur (Bozza *et al.*, 2002; Latgé, 1999; Willey *et al.*, 2011). By contrast, in immunocompromised patients, the spores can germinate into hyphae, invading lung tissue and leading to severe infection with high mortality rates (Bozza *et al.*, 2002; Latgé, 1999; Willey *et al.*, 2011). *A. fumigatus* produces enzymes that damage the respiratory lining, making the lungs more vulnerable to further infections (Portaels *et al.*, 2024). The innate immune system, including components such as the complement system, dendritic cells and neutrophils, is crucial for recognising and eliminating these spores. When these defences are weakened, the risk of invasive aspergillosis increases (Parente *et al.*, 2020; Guo *et al.*, 2020; Balloy and Chignard, 2009). Environmental conditions influence both the number of airborne *Aspergillus* spores and their survival. Temperature affects spore properties: for example, conidia produced at around 25°C have lower heat tolerance yet greater resistance to UV radiation than those formed at higher temperatures (Hagiwara *et al.*, 2017). Higher temperatures in summer are linked to increased airborne spore counts, suggesting a seasonal pattern (Panackal *et al.*, 2010; van Rhijn *et al.*, 2021).

Humidity is also important. Elevated relative humidity can enhance the concentration and viability of airborne *Aspergillus* spores, while the combined effects of temperature and humidity significantly impact overall spore levels (Abdel Hameed *et al.*, 2012; Kim *et al.*, 2025). Airflow and ventilation further influence spore distribution: lower wind speeds and inadequate ventilation can result in higher spore concentrations. This is particularly concerning in hospital settings, where construction or demolition may further increase exposure (Chen *et al.*, 2022; Vonberg and Gastmeier, 2006). UV radiation affects spore viability as well: spores exposed to UV during formation can develop increased resistance, which may alter their potential for airborne transmission (Hagiwara *et al.*, 2017).

Preventing aspergillosis, especially in the nosocomial environment, is challenging due to the difficulty of diagnosing and treating the infection. Effective prevention requires a multifaceted approach involving stringent environmental control measures, such as HEPA (High-Efficiency Particulate Air) filtration, regular air quality maintenance, and construction precautions, along with consistent surveillance and targeted antifungal prophylaxis for high-risk patients. These integrated strategies are fundamental for high-risk hospital areas and during periods of construction or renovation to minimise the risk of fungal exposure and potentially lethal infection (Garnaud *et al.*, 2012; Hajjeh and Warnock, 2001; Suleyman and Alangaden, 2016).

Protists

Protists, particularly parabasalids and amoebae, play a complex and emerging role in respiratory infections, presenting unique challenges to diagnosis and treatment.

Parabasalids are single-celled, flagellated organisms, such as *Lophomonas*, that typically inhabit low-oxygen environments and are characterised by a distinctive internal structure called the parabasal body. In contrast, amoebae, including *Acanthamoeba*, which belong to the Amoebozoa, a group of free-living amoebae found in soil and water, can also cause infections. These organisms can act as primary pathogens or serve as vectors for other infectious agents, complicating treatment and prevention efforts. Parabasalids, such as *Lophomonas*, are emerging as significant respiratory pathogens.

The entry of *Lophomonas* into the respiratory tract occurs through inhalation of cysts present in cockroach faeces and potentially through direct person-to-person transmission via small respiratory droplets (Azizi *et al.*, 2023; Rao *et al.*, 2014). Once in the respiratory system, the multiflagellated trophozoites adhere to the respiratory mucosa leading to symptoms such as chronic cough and asthma-like inflammation. Initially, *Lophomonas* infections were reported predominantly in immunocompromised patients, such as those with HIV/AIDS or those undergoing immunosuppressive treatments (Keche *et al.*, 2022; Nakhaei *et al.*, 2022). However, recent studies have shown that *Lophomonas* can also infect healthy individuals, presenting with symptoms such as fever, productive cough, dyspnoea, and even severe pneumonia (Azizi *et al.*, 2023; Nakhaei *et al.*, 2022). The difficulty in differentiating *Lophomonas* from human bronchial epithelial cells under microscopy, combined with the absence of specific diagnostic tools, often results in misdiagnosis (Keche *et al.*, 2022). Therefore, further research is required to develop reliable diagnostic techniques and effective treatments (Azizi *et al.*, 2023).

Acanthamoeba play a significant role in respiratory infections by acting both as a "trojan horse" that shelters pathogens such as *L. pneumophila* within its cells and as a vector that actively facilitates the transmission of these bacteria from environmental reservoirs to human hosts (Henriquez *et al.*, 2021). In this context, the term "trojan horse" refers to its ability to protect pathogens from adverse conditions, while "vector" highlights its role in the direct delivery and dissemination of these microorganisms. *Acanthamoeba* infections occur when individuals inhale airborne cysts or acquire the protist through contaminated water or soil that it contacts via the nasal passages (Nugraha *et al.*, 2023). Once inhaled, *Acanthamoeba*, which often already harbours pathogenic bacteria from environmental sources, provides a protective niche that shields these bacteria from environmental stressors, including disinfectants (Mooney *et al.*, 2024). They also provide a protective niche for bacteria, including *L. pneumophila* and *Bordetella bronchiseptica*, which use the amoeba as a reservoir and vector to survive hostile environmental conditions and to enter human hosts (Khemasuwan *et al.*, 2014; Nugraha *et al.*, 2023). The relationship between *Acanthamoeba* and these bacteria is mutually advantageous: *Acanthamoeba* feeds on the bacteria for its nutritional needs, while the bacteria use the amoebae as a shield to avoid environmental stress thereby complicating disease prevention efforts.

Additionally, *Entamoeba histolytica* is another protist capable of causing severe respiratory manifestations. For *E. histolytica*, pulmonary involvement typically occurs after the amoeba invades the intestinal mucosa, entering the bloodstream and leading to systemic infection. This can result in abscesses and hepatobronchial fistulas in the lungs, causing significant respiratory issues (Khemasuwan *et al.*, 2014). Beyond amoebae, *Rhinosporidium seeberi*, a Mesomycetozoea, causes rhinosporidiosis, which

can involve the tracheobronchial tree and lead to severe airway obstruction. This often requires medical intervention, including bronchoscopy, to clear the obstruction and manage the infection effectively (Khemasuwan *et al.*, 2014).

The ecological roles of protists in respiratory infections demonstrate a dynamic vastly different from typical bacterial or viral infections. Their ability to act as emerging primary pathogens (*Lophomonas*) or as vectors and amplifiers of other pathogens (*Acanthamoeba, E. histolytica*) creates a multilayered challenge that complicates infection dynamics.

Aeroallergens

An aeroallergen is any airborne biological particle, or bioaerosol, capable of triggering or exacerbating allergic reactions. Outdoor sources commonly include plant pollens and fungal spores, while indoor allergens predominantly arise from pet dander, especially from cats and dogs, and house dust mites (Pashley *et al.*, 2024). Seasonal allergic rhinitis (hay fever) affects a significant proportion of the population, with over 20% of the UK population experiencing symptoms. In Europe, this condition impacts over 80 million adults (24%) and a higher percentage of children (30-40%), with numbers rising annually (Scadding *et al.*, 2017; WHO, 2012).

Aeroallergens gain access to the respiratory system primarily through inhalation. Larger particles, such as intact pollen grains, are usually deposited in the upper airways, leading to conditions like allergic rhinitis. However, smaller allergenic fragments and particulate matter can bypass the upper airway defences, including nasal hairs and the mucociliary escalator, reaching the lower airways and alveoli. Environmental factors, such as humidity, airflow, and pollution, influence their transport and deposition, further complicating exposure dynamics (Brown *et al.*, 2003; Eguiluz-Gracia *et al.*, 2020).

Grass pollen (from the genus *Poaceae*) is one of the most prevalent outdoor aeroallergens, significantly contributing to allergic asthma and rhinitis (D'Amato *et al.*, 2023). During peak pollen seasons, certain grass species release large quantities of allergenic particles, exacerbating respiratory conditions in sensitised individuals (Eguiluz-Gracia *et al.*, 2020). Similarly, birch pollen has been linked to increased asthma hospitalisations, particularly when combined with environmental factors like ozone, which amplify its allergenic potential (Wang *et al.*, 2021). Thunderstorms also aggravate the allergenicity of pollen and spores. Remarkable increases of incidences of asthma have been reported during thunderstorms when gusty winds sweep up pollen and fungal spores and the accompanying sudden increases in humidity cause osmotic shock that rupture pollen grains (mostly pollen of grasses) and fungal spores thereby releasing small granules of their content that can penetrate into the lower respiratory tract (Banasiak *et al*., 2022).

Once inhaled, pollen grains interact with the respiratory epithelium, triggering a cascade of immune responses. This process involves the activation of mast cells and basophils, leading to the release of histamines, cytokines, and leukotrienes. These mediators cause inflammation, airway constriction, and mucus hypersecretion, hallmarks of allergic rhinitis and asthma (Brown *et al.*, 2003). Specifically, when an individual is first exposed to an aeroallergen, their immune system produces IgE antibodies that are specific to that allergen. These IgE antibodies bind to high-affinity IgE receptors on the surfaces of mast cells and basophils, effectively sensitising them for

future exposures (Siraganian, 2003; Vitte *et al.*, 2022). Upon re-exposure, the allergen cross-links the IgE antibodies on the cell surfaces, causing the receptors to aggregate. This aggregation initiates a signalling cascade within the mast cells, leading to their activation and rapid degranulation. As a result, preformed mediators such as histamine are released into the surrounding tissue. Histamine then triggers vasodilation, increases vascular permeability, and causes smooth muscle contraction, which together contribute to the immediate symptoms of allergic reactions, such as itching, swelling, and bronchoconstriction. This IgE-mediated process occurs quickly, typically within minutes of allergen exposure (Ishizaka *et al.*, 1983; Siraganian, 2003; Tanaka and Furuta, 2021) Additionally, proteases in pollen grains can disrupt epithelial tight junctions, increasing susceptibility to other airborne pathogens and pollutants (Ryu *et al.*, 2022). Climate change has exacerbated the impact of grass and birch pollen (*Betula* spp.). Rising temperatures and prolonged growing seasons have led to higher pollen concentrations and longer exposure periods, worsening respiratory symptoms in susceptible populations. Increased air pollution further interacts with pollen, altering its allergenic properties and enhancing its ability to penetrate the respiratory tract (Eguiluz-Gracia *et al.*, 2020; Ryu *et al.*, 2022; Stoian *et al.*, 2024). The interaction between air pollutants and aeroallergens, such as ozone and diesel exhaust particles (DEPs), modifies allergen structure and enhances its bioavailability, heightening the immune response (Lira *et al.*, 2024; Ouyang *et al.*, 2024).

Moreover, pet dander is a common indoor aeroallergen, particularly from cats and dogs. Dander particles are lightweight and remain suspended in the air for long periods, facilitating inhalation. These allergens (Fel d 1 and Can f 1 respectively) are rich in proteins that elicit strong IgE-mediated immune responses. This can lead to airway inflammation, mucus production, and heightened hyper-responsiveness in sensitised individuals (Pashley *et al.*, 2024). Chronic exposure to pet allergens has been associated with worsening asthma symptoms and increased hospitalisations (Brown *et al.*, 2003).

House dust mites (HDM, *Dermatophagoides farina* and *D. pteronyssinus*) are another significant source of indoor allergens. Their allergens, particularly Der f 1 and Der p 1, are proteolytic enzymes capable of disrupting the epithelial barrier, impairing lung defences, and facilitating allergic sensitisation (Brown *et al.*, 2003). HDM allergens have been shown to suppress elastase inhibitors in the lungs, increasing vulnerability to respiratory infections (Ryu *et al.*, 2020). Furthermore, exposure to HDM allergens is a strong predictor of asthma severity, with sensitised individuals experiencing more frequent and severe exacerbations (Eguiluz-Gracia *et al.*, 2020).

Both outdoor and indoor aeroallergens interact with environmental pollutants, compounding their effects on respiratory health. DEPs, for instance, enhance the allergenic potential of pollen and HDM allergens by increasing their deposition in the lower airways and modulating immune responses. Co-exposure to DEPs and aeroallergens has been linked to impaired lung function, increased airway inflammation, and heightened asthma symptoms (Lira *et al.*, 2024; Ryu *et al.*, 2022). Studies have shown that DEPs can act as carriers for aeroallergens, facilitating their penetration deeper into the respiratory tract. This co-exposure amplifies the allergic response and increases oxidative stress and inflammation in the airways, worsening respiratory conditions (Brown *et al.*, 2003; Eguiluz-Gracia *et al.*, 2020). Furthermore, airborne

pollutants such as ozone and nitrogen dioxide modify the structure of allergenic proteins, enhancing their allergenicity and immunogenicity. Ozone exposure has been linked to increased protease activity in pollen grains, making them more capable of disrupting epithelial barriers (Ouyang *et al.*, 2024). Additionally, exposure to particulate matter ($PM_{2.5}$) and nitrogen dioxide in urban environments heightens the risk of allergen-induced respiratory diseases, particularly among populations already sensitised to aeroallergens (Lira *et al.*, 2024). Furthermore, co-exposure to ozone and pollen not only amplifies the allergenic potential of pollen but also contributes to increased airway resistance and reduced lung function (Ouyang *et al.*, 2024). These findings underscore the complex interplay between environmental pollutants and aeroallergens, highlighting the need for integrated approaches to mitigate their health impacts.

In conclusion, outdoor and indoor aeroallergens play a critical role in developing and exacerbating respiratory conditions such as asthma and allergic rhinitis. Climate change, urbanisation, and increased time spent indoors have intensified their impact on public health. Understanding the mechanisms of allergen-induced respiratory diseases and their interactions with environmental pollutants is essential for developing targeted interventions and improving outcomes for affected individuals.

⏩ Conclusions

This chapter highlights significant health impacts of bioaerosols while addressing the uncertainties and challenges that persist in this field. One major challenge lies in understanding the variability in bioaerosol exposure and its resultant health outcomes. The nature of the exposure is a strong driving force for the health impacts. However, it is still unclear how this translates into specific disease risk.

A further challenge in this field is the limitation and influence of current sampling and measurement techniques. These methods often fail to accurately capture the true concentrations and variability of bioaerosols over time and across different environments, making it difficult to directly correlate exposure levels with specific health outcomes The sensitivity of sampled material to the process of capture and handling post deposition requires full understanding of its influence on viability of captured bioaerosol. Subsequently, definitive links between bioaerosol presence and adverse health outcomes need to be established.

The spatial and temporal variability of a range of environmental factors has a profound influence on particle viability and behaviour, which complicates the study of bioaerosol exposure. It is challenging to draw consistent conclusions regarding health outcomes due to diverse biological activities and environmental events.

The variability in host responses to bioaerosol exposure introduces yet another level of uncertainty. Differences in individual susceptibility to inhaled bioaerosols may arise due to genetic predisposition, immune system status, or pre-existing health conditions. Emerging evidence also suggests that the respiratory microbiome plays a key role in modulating responses to bioaerosol exposure, although the precise mechanisms remain poorly understood. Further research could greatly enhance our understanding of individual differences in susceptibility to bioaerosols.

Whilst significant strides have been made in identifying airborne pathogens, bridging the gap between exposure and subsequent health effects requires continued research.

New tools, such as NGS, enable the identification of a broader spectrum of biological materials, including viruses and fungi, from bioaerosol samples. Continued advances in sampling technology, coupled with a multidisciplinary approach incorporating epidemiology and microbiology, are essential for comprehensively understanding the impact of bioaerosols on human health.

The way forward involves refining sampling methodologies, bridging the knowledge gap between exposure and health outcomes, and enhancing our understanding of the variability in host responses and the role of the respiratory microbiome. Addressing these gaps is vital for mitigating the health risks from bioaerosols and developing effective interventions to protect public health in environments where exposure to bioaerosols is unavoidable. Overall, the challenges for research on bioaerosols with effects on human health are common with those for research on bioaerosols that affect other organisms and habitats in Earth's biosphere. Recognition of these common challenges can help build bridges between research and environmental monitoring in the biomedical, environmental and agricultural sciences.

⏩ Literature cited

Adar S.D., *et al*., 2016. The respiratory microbiome: An underappreciated player in the human response to inhaled pollutants? *Ann. Epidemiol.*, 26, 5, 355–359. https://doi.org/10.1016/j.annepidem.2016.03.010

Azizi S., *et al*., 2023. *Lophomonas blattarum* respiratory infection in an immunocompromised patient: A case report from Dubai. *Int. J. Sci. Res. Pub.*, 13 (5), 282-285. https://doi.org/10.29322/IJSRP.13.05.2023.p13736

Balloy V., Chignard M., 2009. The innate immune response to *Aspergillus fumigatus*. *Microbes Infect.*, 11 (12), 919-927. https://doi.org/10.1016/j.micinf.2009.07.002

Banasiak N.C., *et al*., 2022. The perfect storm: Thunderstorm-related asthma. *J. Nurse Pract.*, 18, 339-402. https://doi.org/10.1016/j.nurpra.2021.06.008

Barbuti S., *et al*., 2002. *Igiene* (Second Edition). Monduzzi Editore, 484 p.

Bonaventura A., *et al*., 2021. Endothelial dysfunction and immunothrombosis as key pathogenic mechanisms in COVID-19. *Nature Reviews Immunology*, 21 (5), 319-329. https://doi.org/10.1038/s41577-021-00536-9

Bozza S., *et al*., 2002. Dendritic cells transport conidia and hyphae of *Aspergillus fumigatus* from the airways to the draining lymph nodes and initiate disparate Th responses to the fungus. *J. Immunol.*, 168 (3), 1362-1371. https://doi.org/10.4049/jimmunol.168.3.1362

Brown A., *et al*., 2003. House dust mite Der p 1 downregulates defenses of the lung by inactivating elastase inhibitors. *Am. J. Respir. Cell. Mol. Biol.,* 29 (3), 381-389. https://doi.org/10.1165/rcmb.2003-0060OC

Bustos I.G., *et al*., 2023. Exploring the complex relationship between the lung microbiome and ventilator-associated pneumonia. *Expert Rev. Respir. Med.*, 17 (10), 889-901. https://doi.org/10.1080/17476348.2023.2273424

Chauhan D., Shames S.R., 2021. Pathogenicity and virulence of *Legionella*: Intracellular replication and host response. *Virulence*, 12 (1), 1122-1144. https://doi.org/10.1080/21505594.2021.1903199

Chen Y.C., *et al.*, 2022. Air sampling for fungus around hospitalized patients with coronavirus disease 2019. *Journal of Fungi*, 8 (7), 692. https://doi.org/10.3390/jof8070692

Clopper B.R., *et al*., 2021. A methodology for classifying root causes of outbreaks of Legionnaires' disease: Deficiencies in environmental control and water management. *Microorganisms,* 9 (1), 89. https://doi.org/10.3390/MICROORGANISMS9010089

Cunha B.A., *et al*., 2016. Legionnaires' disease. *Lancet*, 387 (10016), 376-385. https://doi.org/10.1016/S0140-6736(15)60078-2

Dabisch P., *et al*., 2021. The influence of temperature, humidity, and simulated sunlight on the infectivity of SARS-CoV-2 in aerosols. *Aerosol Sci. Technol.*, 55 (2), 142-153. https://doi.org/10.1080/02786826.2020.1829536

D'Amato G., *et al*., 2023. Pollen respiratory allergy: Is it really seasonal? *World Allergy Organ. J.*, 16 (7), 100799. https://doi.org/10.1016/j.waojou.2023.100799

da Silva P.G., *et al.*, 2021. Airborne spread of infectious SARS-CoV-2: Moving forward using lessons from SARS-CoV and MERS-CoV. *Sci. Tot. Environ*, 764, 142802. https://doi.org/10.1016/j.scitotenv.2020.142802

Deeb S., *et al*., 2023. Exploring the effects of ventilation and air-conditioned environments, on droplet and airborne transmission of SARS-COV-2. *Int. J. Innovative Res. Sci. Studies*, 6 (2), 301-309. https://doi.org/10.53894/ijirss.v6i2.1389

de Gabory L., *et al*., 2020. The influenza virus, SARS-CoV-2, and the airways: Clarification for the otorhinolaryngologist. *Eur. Ann. Otorhinolaryngol. Head Neck Dis.,* 137 (4), 291-296. https://doi.org/10.1016/j.anorl.2020.05.015

Dey B., Bishai W.R., 2014. Crosstalk between *Mycobacterium tuberculosis* and the host cell. *Seminars in Immunology*, 26 (6), 486-496. https://doi.org/10.1016/j.smim.2014.09.002

di Giorgio C., *et al*., 1996. Atmospheric pollution by airborne microorganisms in the city of Marseilles. *Atmos. Environ.*, 30 (1), 155-160, https://doi.org/10.1016/1352-2310(95)00143-M

Dutta N.K., Karakousis P.C., 2014. Latent tuberculosis infection: Myths, models, and molecular mechanisms. *Microbiol. Mol. Biol. Rev.*, 78 (3), 343-371. https://doi.org/10.1128/MMBR.00010-14

Eguiluz-Gracia I., *et al*., 2020. The need for clean air: The way air pollution and climate change affect allergic rhinitis and asthma. *Allergy*, 75 (9), 2170-2184. https://doi.org/10.1111/all.14177

Esneau C., *et al*., 2022. Understanding rhinovirus circulation and impact on illness. *Viruses*, 14 (1), 141. https://doi.org/10.3390/V14010141

Estes R.J., Meduri G.U., 1995. The pathogenesis of ventilator-associated pneumonia: I. Mechanisms of bacterial transcolonization and airway inoculation. *Intensive Care Medicine*, 21 (4), 365-383. https://doi.org/10.1007/BF01705418

Fagade O.E., *et al*., 2023. Fate and transport of microorganisms in the air. *In*: Ilori M.O., *et al*., (eds), *Aeromicrobiology Developments in Applied Microbiology and Biotechnology.,* Academic Press, 39-58. https://doi.org/10.1016/B978-0-323-96122-6.00006-2

Fang Z., *et al*., 2007. Culturable airborne bacteria in outdoor environments in Beijing, China. *Microb. Ecol.,* 54, 487-496. https://doi.org/10.1007/s00248-007-9216-3

Finsel I., Hilbi H., 2015. Formation of a pathogen vacuole according to *Legionella pneumophila*: How to kill one bird with many stones. *Cell. Microbiol.*, 17 (7), 935-950. https://doi.org/10.1111/cmi.12450

Fleming A., 1947. Louis Pasteur. *Br. Med. J.*, 1:517. https://doi.org/10.1136/bmj.1.4502.517

Flynn J.L., Chan J., 2001. Immunology of Tuberculosis. *Annu. Rev. Immunol.*, 19 (1), 93-129. https://doi.org/10.1146/annurev.immunol.19.1.93

Flynn J.L., Chan J., 2003. Immune evasion by *Mycobacterium tuberculosis*: Living with the enemy. *Curr. Opin. Immunol.*, 15 (4), 450-455. https://doi.org/10.1016/S0952-7915(03)00075-X

Foat T.G., *et al*., 2022. Modeling the effect of temperature and relative humidity on exposure to SARS-CoV-2 in a mechanically ventilated room. *Indoor Air*, 32 (11). https://doi.org/10.1111/ina.13146

Frank K., Paust, S., 2020. Dynamic natural killer cell and T cell responses to influenza infection. *Front. Cell. Infect. Microbiol.*, 10. https://doi.org/10.3389/fcimb.2020.00425

Garnaud C., *et al*., 2012. Seven-year surveillance of nosocomial invasive aspergillosis in a French University Hospital. *J. Infect.*, 65 (6), 559-567. https://doi.org/10.1016/j.jinf.2012.08.006

Gomez G.B., *et al*., 2021. Uncertain effects of the pandemic on respiratory viruses. *Science*, 372:1043-1044. https://doi.org/10.1126/science.abh3986

Guo Y., *et al*., 2020. During *Aspergillus* infection, monocyte-derived DCs, neutrophils, and plasmacytoid DCs enhance innate immune defense through CXCR3-dependent crosstalk. *Cell Host Microbe*, 28 (1), 104-116.e4. https://doi.org/10.1016/j.chom.2020.05.002

Hagiwara D., *et al*., 2017. Temperature during conidiation affects stress tolerance, pigmentation, and trypacidin accumulation in the conidia of the airborne pathogen *Aspergillus fumigatus*. *PLOS ONE*, *12* (5), e0177050. https://doi.org/10.1371/journal.pone.0177050

Hajjeh R.A., Warnock D.W., 2001. Counterpoint: Invasive Aspergillosis and the Environment—Rethinking Our Approach to Prevention. *Clin. Infect. Dis.*, 33 (9), 1549-1552. https://doi.org/10.1086/322970

Hameed A.A., *et al.*, 2012. Study on some factors affecting survivability of airborne fungi. *Sci. Tot. Environ*, 414, 696-700. https://doi.org/10.1016/j.scitotenv.2011.10.042

Hemmes J.H., *et al*., 1960. Virus survival as a seasonal factor in influenza and poliomyelitis. *Nature*, 188 (4748), 430-431. https://doi.org/10.1038/188430a0

Henriquez F.L., *et al*., 2021. Paradigms of protist/bacteria symbioses affecting human health: *Acanthamoeba* species and *Trichomonas vaginalis*. *Front. Microbiol.*, 11. https://doi.org/10.3389/fmicb.2020.616213

Hu W., *et al*., 2020. Biological aerosol particles in polluted regions. *Current Pollution Reports,* 6, 65-89. https://doi.org/10.1007/s40726-020-00138-4

Huffman J.A., *et al*., 2020. Real-time sensing of bioaerosols: Review and current perspectives. *Aerosol Sci. Technol.*, 54 (5), 465-495. https://doi.org/10.1080/02786826.2019.1664724

Iliadi V., *et al*., 2022. *Legionella pneumophila*: The Journey from the environment to the blood. *Journal of Clinical Medicine*, 11 (20), 6126. https://doi.org/10.3390/jcm11206126

Ishizaka T., *et al*., 1983. Biochemical analysis of initial triggering events of IgE-mediated histamine release from human lung mast cells. *J. Immunol.,* 130 (5), 2357-2362. https://doi.org/10.4049/jimmunol.130.5.2357

Iwasaki A., Pillai P.S., 2014. Innate immunity to influenza virus infection. *Nat. Rev. Immunol.*, 14 (5), 315-328. https://doi.org/10.1038/nri3665

Jackson C.B., *et al*., 2022. Mechanisms of SARS-CoV-2 entry into cells. *Nat. Rev. Mol. Cell Biol.*, 23 (1), 3-20. https://doi.org/10.1038/s41580-021-00418-x

Javanian M., *et al*., 2021. A brief review of influenza virus infection. *J. Medical Virology*, 93 (8), 4638-4646. https://doi.org/10.1002/jmv.26990

Jeong S.B., *et al*., 2022. Size distribution and concentration of indoor culturable bacterial and fungal bioaerosols. *Atmos. Environ. X*, 15, 100182, https://doi.org/10.1016/j.aeaoa.2022.100182

Kannadan A., 2018. History of the miasma theory of disease. *ESSAI*, 16 (18). https://dc.cod.edu/essai/vol16/iss1/18

Kaplan G., *et al*., 2003. *Mycobacterium tuberculosis* growth at thecavity surface: A microenvironment with failed immunity. *Infect. Immunity*, 71 (12), 7099-7108. https://doi.org/10.1128/IAI.71.12.7099-7108.2003

Karra S., *et al*., 2011. The dispersion of traffic related pollutants across a non-homogeneous street canyon. *Procedia Environmental Sciences*, 4, 25-34. https://doi.org/10.1016/j.proenv.2011.03.004

Keche A., *et al*., 2022. Detection of a *Lophomonas*, a rare pathogen in Bronchoalveolar lavage. *Tropical Parasitology*, 12 (2), 124-126. https://doi.org/10.4103/tp.tp_97_21

Kelly F.J., Fussell J.C., 2020. Toxicity of airborne particles—established evidence, knowledge gaps and emerging areas of importance. *Philos. Trans. R. Soc. A Mathematical, Physical and Engineering Sciences*, 378 (2183), 20190322. https://doi.org/10.1098/rsta.2019.0322

Khan A.I., 2013. Characterizing the variability in respirable dust exposure using Johnson transformation and re-examining 2010 proposed changes to the U.S. underground coal mine dust standard. Master's Thesis, University of Kentucky, USA. https://uknowledge.uky.edu/mng_etds/5/

Khemasuwan D., *et al*., 2014. Parasites of the air passages. *Chest*, 145 (4), 883-895. https://doi.org/10.1378/chest.13-2072

Kim D., *et al*., 2025. Revisiting the joint effect of temperature and relative humidity on airborne mold and bacteria concentration in indoor environment: A machine learning approach. *Building and Environment*, 270, 112548. https://doi.org/10.1016/j.buildenv.2025.112548

Kreijtz J.H.C.M., *et al*., 2011. Immune responses to influenza virus infection. *Virus Res.*, 162 (1-2), 19-30. https://doi.org/10.1016/j.virusres.2011.09.022

Kumar S.S., Ghosh A.R., 2019. Assessment of bacterial viability: A comprehensive review on recent advances and challenges. *Microbiology*, 165 (6), 593-610. https://doi.org/10.1099/mic.0.000786

Latgé J.-P., 1999. *Aspergillus fumigatus* and Aspergillosis. *Clin. Microbiol. Rev.*, 12 (2), 310-350. https://doi.org/10.1128/CMR.12.2.310

Lira G., *et al*., 2024. Avoidance of inhaled pollutants and irritants in asthma from a salutogenic perspective. *J. Asthma Allergy*, 17, 237-250. https://doi.org/10.2147/JAA.S445864

Liu X., Shin S., 2019. Viewing *Legionella pneumophila* pathogenesis through an immunological lens. *J. Mol. Biol.*, 431 (21), 4321-4344. https://doi.org/10.1016/j.jmb.2019.07.028

Ljubin-Sternak S., Meštrović T., 2023. Rhinovirus—A true respiratory threat or a common inconvenience of childhood? *Viruses*, 15 (4), 825. https://doi.org/10.3390/V15040825

Löndahl J., Alsved M., 2022. Abrupt decreases in infectivity of SARS-CoV-2 in aerosols. *Proc. Natl Acad. Sci. USA*, 119 (29). https://doi.org/10.1073/pnas.2208742119

Lowen A.C., *et al*., 2007. Influenza virus transmission is dependent on relative humidity and temperature. *PLoS Pathogens*, 3 (10), e151. https://doi.org/10.1371/journal.ppat.0030151

Mainelis G., 2020. Bioaerosol sampling: Classical approaches, advances, and perspectives. *Aerosol Sci. Technol.*, 54 (5), 496-519. https://doi.org/10.1080/02786826.2019.1671950

Małecka-Adamowicz M., *et al*., 2020. Diversity of bioaerosols in selected rooms of two schools and antibiotic resistance of isolated staphylococcal strains (Bydgoszcz, Poland), A case study. *Atmosphere*, 11 (10), 1105. https://doi.org/10.3390/atmos11101105

Mao Y., *et al*., 2022. Independent and interactive effects of environmental conditions on aerosolized surrogate SARS-CoV-2—Beijing, China, June to September 2020. *China CDC Weekly*, 4 (26), 565. https://doi.org/10.46234/ccdcw2022.123

Marple V.A., 2004. History of impactors—The first 110 years. *Aerosol Sci. Technol.*, 38 (3), 247-292. https://doi.org/10.1080/02786820490424347

Marr L.C., *et al*., 2019. Mechanistic insights into the effect of humidity on airborne influenza virus survival, transmission and incidence. *J. R. Soc. Interface*, 16 (150), 20180298. https://doi.org/10.1098/rsif.2018.0298

Martin T.R., 2000. Recognition of bacterial endotoxin in the lungs. *American J. Respiratory Cell Mol. Biol.*, 23 (2), 128-132. https://doi.org/10.1165/ajrcmb.23.2.f189

Meftahi G.H., *et al*., 2020. The possible pathophysiology mechanism of cytokine storm in elderly adults with COVID-19 infection: The contribution of "inflame-aging." *Inflammation Research*, 69 (9), 825-839. https://doi.org/10.1007/s00011-020-01372-8

Mifsud E.J., *et al*., 2021. Innate immune responses to influenza virus infections in the upper respiratory tract. *Viruses*, 13 (10), 2090. https://doi.org/10.3390/v13102090

Mooney R., *et al*., 2024. Acanthamoeba as a protective reservoir for *Pseudomonas aeruginosa* in a clinical environment. *J. Hosp. Infect.*, 153, 21-29. https://doi.org/10.1016/j.jhin.2024.08.010

Morawska L., *et al*., 2022. The physics of respiratory particle generation, fate in the air, and inhalation. *Nat. Rev. Physics*, 4 (11), 723-734. https://doi.org/10.1038/s42254-022-00506-7

Nakhaei M., *et al*., 2022. Global status of emerging *Lophomonas* infection: A systematic review of reported cases (1993-2020). *Interdiscip. Perspect. Infect. Dis.*, 3155845. https://doi.org/10.1155/2022/3155845

Naujoks J., *et al*., 2018. Innate sensing and cell-autonomous resistance pathways in *Legionella pneumophila* infection. *Int. J. Med. Microbiol.*, 308 (1), 161-167. https://doi.org/10.1016/j.ijmm.2017.10.004

Newton H.J., *et al*., 2010. Molecular pathogenesis of infections caused by *Legionella pneumophila*. *Clin. Microbiol. Rev.*, 23 (2), 274-298. https://doi.org/10.1128/CMR.00052-09

Ni J., *et al*., 2024. Concentration, pathogenic composition, and exposure risks of bioaerosol in large indoor public environments: A comparative study of urban and suburban areas. *Sci. Tot. Environ*, 957, 177790, https://doi.org/10.1016/j.scitotenv.2024.177790

Nugraha D.K., *et al*., 2023. Survival of *Bordetella bronchiseptica* in *Acanthamoeba castellanii*. *Microbiology Spectrum*, 11 (2), e00487-23. https://doi.org/10.1128/spectrum.00487-23

Núñez A., *et al*., 2016. Monitoring of airborne biological particles in outdoor atmosphere. Part 2: Metagenomics applied to urban environments. *Int. Microbiol.*, 19 (2), 69-80. https://doi.org/10.2436/20.1501.01.265

Olatunji A.O., Olaboye J.A., 2024. Environmental microbiology and public health: Advanced strategies for mitigating waterborne and airborne pathogens to prevent disease. *Int. Med. Sci. Res. J.*, 4 (7) 756-770 https://doi.org/10.51594/imsrj.v4i7.1355

Ouyang X., *et al*., 2024. Airborne indoor allergen serine proteases and their contribution to sensitisation and activation of innate immunity in allergic airway disease. *Eur. Respir. Rev.*, 33 (172), 230126. https://doi.org/10.1183/16000617.0126-2023

Pai M., *et al*., 2016. Tuberculosis. *Nat. Rev? Dis. Primers*, 2 (1), 1-23. https://doi.org/10.1038/nrdp.2016.76

Panackal A.A., *et al*., 2010. Geoclimatic influences on invasive aspergillosis after hematopoietic stem cell transplantation. *Clin. Infect. Dis.*, 50 (12), 1588-1597. https://doi.org/10.1086/652761

Parente R., *et al*., 2020. The complement system in *Aspergillus fumigatus* infections and its crosstalk with pentraxins. *FEBS Letters*, 594 (16), 2480-2501. https://doi.org/10.1002/1873-3468.13744

Pashley C., *et al*., 2024. Health Effects of Climate Change (HECC) in the UK: 2023 report. Chapter 6: Outdoor airborne allergenic pollen & fungal spores. Centre for Climate and Health Security, and UK Health Security Agency. 58 p. https://www.gov.uk/guidance/health-effects-of-climate-change-hecc-report

Peci A., *et al*., 2019. Effects of absolute humidity, relative humidity, temperature, and wind speed on influenza activity in Toronto, Ontario, Canada. *Appl. Environ. Microbiol.*, 85 (6), e02426-18. https://doi.org/10.1128/AEM.02426-18

Peteranderl C., *et al*., 2016. Human influenza virus infections. *Seminars in Respiratory and Critical Care Medicine*, 37 (04), 487-500. https://doi.org/10.1055/s-0036-1584801

Pleil J.D., *et al*., 2021. The physics of human breathing: Flow, timing, volume, and pressure parameters for normal, on-demand, and ventilator respiration. *J. Breath Res.*, 15 (4), 042002. https://doi.org/10.1088/1752-7163/ac2589

Portaels J., *et al*., 2024. *Aspergillus fumigatus* spore proteases alter the respiratory mucosa architecture and facilitate equine Herpesvirus 1 infection. *Viruses*, 16 (8), 1208. https://doi.org/10.3390/v16081208

Rahlwes K.C., *et al*., 2023. Pathogenicity and virulence of *Mycobacterium tuberculosis*. *Virulence*, 14 (1). https://doi.org/10.1080/21505594.2022.2150449

Rao X., *et al*., 2014. Retrospect and prospect of *Lophomonas blattarum* infections and lophomoniasis reported in China. *Open Access Library Journal*, 1 (9), 1. https://doi.org/10.4236/oalib.1101121

Richard M., *et al*., 2020. Influenza A viruses are transmitted via the air from the nasal respiratory epithelium of ferrets. *Nat. Comm.*, 11 (1), 766. https://doi.org/10.1038/s41467-020-14626-0

Robertson S., *et al*., 2019. Bioaerosol exposure from composting facilities and health outcomes in workers and in the community: A systematic review update, *Int. J. Hyg. Environ. Health*, 222 (3), 364-386. https://doi.org/10.1016/j.ijheh.2019.02.006

Robey A.J., Fierce L., 2022. Sensitivity of airborne transmission of enveloped viruses to seasonal variation in indoor relative humidity. *International Communications in Heat and Mass Transfer*, 130, 105747. https://doi.org/10.1016/j.icheatmasstransfer.2021.105747

Ryu M.H., *et al*., 2020. Particle depletion of diesel exhaust restores allergen-induced lung-protective surfactant protein D in human lungs. *Thorax*, 75 (8), 640-647. https://doi.org/10.1136/thoraxjnl-2020-214561

Ryu M.H., *et al*., 2022. Urinary eicosanoid levels reflect allergen and diesel exhaust coexposure and are linked to impaired lung function. *Environ. Sci. Technol.*, 56 (11), 7107-7118. https://doi.org/10.1021/acs.est.1c07268

Scadding G.K., *et al*., 2017. BSACI guideline for the diagnosis and management of allergic and non-allergic rhinitis. *Clin. Exp. Allergy*, 47 (7), 856-889. https://doi.org/10.1111/cea.12953

Scheff P.A., *et al*., 2000. Indoor air quality in a middle school, Part II: Development of emission factors for particulate matter and bioaerosols. *Appl. Occup. Environ. Hyg.*, 15 (11), 835-842. https://doi.org/10.1080/10473220050175715

Scheuch G., 2020. Breathing is enough: For the spread of influenza virus and SARS-CoV-2 by breathing only. *J. Aerosol Med. Pulm. Drug Deliv.*, 33 (4), 230-234. https://doi.org/10.1089/jamp.2020.1616

Singer B.D., 2020. COVID-19 and the next influenza season. *Sci. Adv.*, 6 (31). https://doi.org/10.1126/sciadv.abd0086

Siraganian R., 2003. Mast cell signal transduction from the high-affinity IgE receptor. *Curr. Opin. Immunol.*, 15 (6), 639-646. https://doi.org/10.1016/j.coi.2003.09.010

Smith K.A., 2012. Louis Pasteur, the father of immunology? *Front. Immunol.*, 3, 68. https://doi.org/10.3389/fimmu.2012.00068

Sooryanarain H., Elankumaran S., 2015. Environmental role in influenza virus outbreaks. *Annu. Rev. Anim. Biosci.*, 3 (1), 347-373. https://doi.org/10.1146/annurev-animal-022114-111017

Stettler M.E.J., *et al*., 2022. Source terms for benchmarking models of SARS-CoV-2 transmission via aerosols and droplets. *R. Soc. Open Sci.*, 9:5. https://doi.org/10.1098/rsos.212022

Stoian I.M., *et al*., 2024. Relationship between climate change, air pollution and allergic diseases caused by *Ambrosia artemisiifolia* (Common Ragweed). *Maedica*, 19 (1), 94-105. https://doi.org/10.26574/maedica.2024.19.1.94

Suleyman G., Alangaden G.J., 2016. Nosocomial fungal infections. *Infect. Dis. Clin. North Am.*, 30 (4), 1023-1052. https://doi.org/10.1016/j.idc.2016.07.008

Swanson M.S., Hammer B.K., 2000. *Legionella pneumophila* pathogenesis: A fateful journey from amoebae to macrophages. *Annu. Rev. Microbiol.*, 54 (1), 567-613. https://doi.org/10.1146/annurev.micro.54.1.567

Sykes D., 2005. The development of a bioaerosol sampler for the detection of enzymes in industry. Doctoral dissertation, School of Science and Technology, University of Teesside.

Tanaka S., Furuta K., 2021. Roles of IgE and histamine in mast cell maturation. *Cells*, 10 (8), 2170. https://doi.org/10.3390/cells10082170

Thornton G.M., *et al*., 2022. The impact of heating, ventilation, and air conditioning design features on the transmission of viruses, including the 2019 novel coronavirus: A systematic review of ultraviolet radiation. *PLoS One*, 17 (4), e0266487. https://doi.org/10.1371/journal.pone.0266487

Tian W., *et al*., 2020. Immune suppression in the early stage of COVID-19 disease. *Nat. Comm.*, 11 (1), 5859. https://doi.org/10.1038/s41467-020-19706-9

Trastoy R., *et al*., 2018. Mechanisms of bacterial tolerance and persistence in the gastrointestinal and respiratory environments. *Clin. Microbiol. Rev.*, 31 (4). https://doi.org/10.1128/CMR.00023-18

van Rhijn N., *et al*., 2021. Meteorological factors influence the presence of fungi in the air; A 14-month surveillance study at an adult cystic fibrosis center. *Front. Cell. Infect. Microbiol.*, 11. https://doi.org/10.3389/fcimb.2021.759944

Vitte J., *et al*., 2022. Fungal exposome, human health, and unmet needs: A 2022 update with special focus on allergy. *Allergy*, 77 (11), 3199-3216. https://doi.org/10.1111/all.15483

Vonberg R-P., Gastmeier P., 2006. Nosocomial aspergillosis in outbreak settings. *J. Hosp. Infect.*, 63 (3), 246-254. https://doi.org/10.1016/j.jhin.2006.02.014

Wang C.C., *et al*., 2021. Airborne transmission of respiratory viruses. *Science*, 373 (6558). https://doi.org/10.1126/science.abd9149

Wang W., *et al*., 2022. Internal exposure and distribution of airborne fine particles in the human body: Methodology, current understandings, and research needs. *Environ. Sci. Technol.*, 56 (11), 6857-6869. https://doi.org/10.1021/acs.est.1c07051

Wei K., *et al*., 2020. Distinction of two kinds of haze. *Atmos. Environ.*, 223:117228. https://doi.org/10.1016/j.atmosenv.2019.117228

Whitby C., *et al*., 2022. Compendium of analytical methods for sampling, characterization and quantification of bioaerosols. *Adv. Ecol. Res.*, 67, 101-229. https://doi.org/10.1016/bs.aecr.2022.09.004

WHO, 2012. Atlas of health and climate. https://www.who.int/publications/i/item/9789241564526

WHO., 2022. Billions of people still breathe unhealthy air: New WHO data. https://www.who.int/news/item/04-04-2022-billions-of-people-still-breathe-unhealthy-air-new-who-data

WHO., 2024. Health consequences of air pollution. https://www.who.int/news/item/25-06-2024-what-are-health-consequences-of-air-pollution-on-populations

Willey J.M., *et al*., 2011. *Prescott's microbiology*. McGraw-Hill Higher Education, New York, NY, 1070 p.

Wu T., *et al*., 2018. Infant and adult inhalation exposure to resuspended biological particulate matter. *Environ. Sci. Technol.*, 52 (1), 237-247. https://doi.org/10.1021/acs.est.7b04183

Xie S., *et al*., 2003. Spatial distribution of traffic-related pollutant concentrations in street canyons. *Atmos. Environ.*, 37 (23), 3213-3224. https://doi.org/10.1016/S1352-2310(03)00321-2

Xie W., *et al*., 2021. The source and transport of bioaerosols in the air: A review. *Front. Environ. Sci. Eng*., 15 (3), 44. https://doi.org/10.1007/s11783-020-1336-8

Xu R., *et al*., 2021. Weather, air pollution, and SARS-CoV-2 transmission: A global analysis. *Lancet Planetary Health*, 5 (10), e671-e680. https://doi.org/10.1016/S2542-5196(21)00202-3

Yang W., Marr L.C., 2011. Dynamics of airborne influenza A viruses indoors and dependence on humidity. *PloS ONE*, 6 (6), e21481. https://doi.org/10.1371/journal.pone.0021481

Yazid A.W.M., *et al*., 2014. A review on the flow structure and pollutant dispersion in urban street canyons for urban planning strategies. *Simulation*, 90 (8), 892-916. https://doi.org/10.1177/0037549714528046

Yesudhas D., *et al*., 2021. COVID-19 outbreak: History, mechanism, transmission, structural studies and therapeutics. *Infection*, 49 (2), 199-213. https://doi.org/10.1007/s15010-020-01516-2

Yin Y., *et al*., 2023. Effects and interaction of temperature and relative humidity on the trend of influenza prevalence: A multi-central study based on 30 provinces in mainland China from 2013 to 2018. *Infectious Disease Modelling*, 8 (3), 822-831. https://doi.org/10.1016/j.idm.2023.07.005

Zhai W., *et al*., 2019. The immune escape mechanisms of *Mycobacterium tuberculosis*. *Int. J. Mol. Sci.*, 20 (2), 340. https://doi.org/10.3390/ijms20020340

Chapter 14

Using the logic of aerial dissemination patterns and networks for optimizing plant disease surveillance strategies

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The problem of surveillance

This chapter introduces a problem that has challenged human comprehension of plant pathology processes and capacity for producing crop protection tools for millennia (Mahaffee and Stoll, 2016). In previous parts of the book, the notion of long-distance dispersal has been introduced, which may involve transport events of several thousands of kilometers (Brown and Hovmøll, 2002). This dispersal, from an epidemiological perspective, translates into an increased probability of invasion (*sensu* Xing *et al.*, 2020) of airborne pathogens that act as external inoculum to cultivated areas, with increasing implications for crop and human health (Aylor, 2017).

The aerial transport of spores and bacteria has repeatedly proven to be a persistent challenge in plant protection. Unlike overwintering pathogens, which can persist during unfavorable seasons, whose impact may be mitigated by removing local sources of infection (Bryde and Willets, 1977), very few actions can be taken to contain the arrival of a wind-driven invisible enemy. Consequently, strategies to control the spread of airborne diseases, when possible, are based on the preventive application of biocides, with important impacts on the environment, human health, and increased costs (Yadav and Devi, 2017). Moreover, with the homogenization of crops, the spread of airborne plant pathogens to new territories has accelerated significantly in recent decades. This is revealed by the spread of soybean rust from South to North America, or the spread of stem rust of wheat from the Middle East to Africa and Europe (Corredor-Moreno and Saunders, 2020).

Under these circumstances, it has become essential to enhance existing strategies for plant disease surveillance (Ristaino *et al.*, 2021). Epidemic surveillance is the discipline that focuses on methods for detecting, as early as possible, the introduction of a pest, pathogen, or alien species in a new susceptible area; or, once introduced, to monitor its health status and contain the outbreak area. The increasing number of emerging plant pathogens across vast and complex agricultural landscapes has necessitated the development of sophisticated, efficient and international strategies, such as the RustTracker

initiative for wheat rusts[10]. This need motivates the increased use of statistical techniques (e.g., the rule-of-tree approximation; Parnell *et al.*, 2017), as they provide scientifically-grounded metrics and standards for sampling (monitoring) a limited number of highly-representative individuals (surveilled units) within large populations (all susceptible hosts). Established techniques include risk assessment (Ristaino *et al.*, 2021) to identify areas with higher infectious potential and epidemiologically-driven surveillance, based on known epidemic dynamics.

In the case of an airborne epidemic spread, the epidemic is shaped geographically by wind-driven transmission of the disease between host units. It is noteworthy that, besides challenging the estimation of airborne microbial infections dispersed over long distances, the same mechanism of atmospheric dispersion can be used to design surveillance strategies (Visser *et al.*, 2019). Recent scientific advances provide new tools to improve our understanding of atmospheric biogeography and the atmospheric connectivity of landmasses. In this chapter, we will present the fundamental notions and most recent discoveries about airborne transport of plant diseases, focusing on the methods and tools that can be used to improve epidemic surveillance.

The first section is devoted to atmospheric biogeography, an emerging field focused on describing the spatial diversity of life in the air and the processes that shape that diversity. The second section describes how atmospheric connectivity networks can be constructed to characterize possible epidemiological links between distant areas. We conclude by addressing the problem of cooperation across geopolitical boundaries when dealing with the surveillance of rapidly spreading diseases whose dispersal knows no borders.

⏩ Atmospheric biogeography as a tool to investigate pathogen distribution

Biogeography is the discipline that deals with the geographic distribution of living organisms and their variation across space and time. Historically, biogeography has predominantly focused on terrestrial and aquatic environments (Sommeria-Klein *et al.*, 2021), while relatively little attention has been devoted to the atmosphere (Womack *et al.*, 2010). Nonetheless, recent discoveries point towards a holistic interpretation of biogeography, encompassing all realms of Earth.

Atmospheric biogeography is mostly concerned with microbial life, the predominant form of life in the air. Indeed, under the right circumstances, several thousands of organisms from hundreds of different species can be found in small volumes of air, in numbers similar to those found in other environments, like soil (Brodie *et al.*, 2007). Most aerobiology research has investigated the existence of patterns in microbial density (Burrows *et al.*, 2009), either across time or space. Longitudinal studies have found that microbial densities at a given location show temporal trends that can be either seasonal, especially at mid-latitudes (Bertolini *et al.*, 2013; Bowers *et al.*, 2013; Cáliz *et al.*, 2018; Fröhlich-Nowoisky *et al.*, 2009; Tignat-Perrier *et al.*, 2020) or diel (Fierer *et al.*, 2008; Gusareva *et al.*, 2019; Oneto *et al.*, 2020). Across space, evidence of distribution patterns is more elusive, as found by the few studies that included multiple sampling locations. It appears that microbial communities are

10. CIMMYT (2019). https://rusttracker.cimmyt.org/. A Global Wheat Rust Monitoring System.

highly variable, with geographical patterns explained mostly by climatic and environmental factors (Barberán *et al.*, 2015). Nonetheless, certain microbial species seem to be more widespread than other, independently of the presence of local sources, and that is particularly true for species displaying metabolic traits relevant to survival in air, such as the ability to form spores (Archer *et al.*, 2022).

One of the most remarkable biogeographic patterns is the presence of distinct biogeographic regions, i.e. large and distinct areas of the Earth's surface that are defined by unique combinations of living organisms. These regions are characterized by their specific biota, which are adapted to the particular environmental conditions of the area. The boundaries of biogeographic regions are determined by various factors, including climate, geography, and historical events, which influence the distribution and diversity of species. The concept of atmospheric biogeographic regions has been proposed relatively recently (Womack *et al.*, 2010) and, at present, their existence remains largely unknown. Nonetheless, recent studies have found that airborne fungi show pronounced geographic patterns at global scales, with marked differences between land and sea environments (Fröhlich-Nowoisky *et al.*, 2012) as well as the existence of rather pristine and isolated biogeographic regions, such as the Southern Ocean atmospheric boundary layer (Uetake *et al.*, 2020). An analytical tool has been recently proposed (Kling and Ackerly, 2020) based on the reconstruction of atmospheric patterns and inspired by an analogy with hydrology, that of *windsheds* (Box 14.1). This new instrument offers the promise of significant advancements in the

Box 14.1: Windsheds

Windsheds are the atmospheric equivalent of watersheds in hydrography. Just as any location on a landscape has an upstream watershed and a downstream delta, it also has an upwind and downwind dispersal catchment representing areas of likely inbound and outbound wind dispersal (Kling and Ackerly, 2020, 2021). The main difference is that windsheds are much more elusive than watersheds, rarely changing due to abrupt landscape modifications (either natural or human-mediated) or because of slow natural earth processes. The inbound windshed of a given region is defined as the set of all upwind locations from where air masses can travel to the destination, and similarly for downwind location and outbound windsheds. Theoretically, there is no geographical limit to the extent of a windshed, as air masses are constantly moving, potentially connecting any two given locations on the planet given enough time. Nonetheless, not all points within a windshed are equidistant, as long-term atmospheric patterns depend on the local distribution of instantaneous wind conditions at a site, in particular wind speed, prevailing wind direction and wind anisotropy (Kling and Ackerly, 2020). Hence, sites within a windshed can be characterized by their proximity to the source/sink location in terms of average travel time. In Figure 14.1 we show the inbound and outbound windsheds (in red and blue respectively) of two locations in Europe, Milan and Avignon, comprising all sites within 100 hours of average wind travel time to and from the two sites*. In yellow, we highlight those locations that belong to the intersection of inbound and outbound windsheds. The windsheds around Milan (inbound ~70 K km^2, outbound ~28 K km^2) are smaller than the one around Avignon (inbound ~168 K km^2, outbound ~416 K km^2), most likely due to the orography of the Po Valley of Northern Italy, surrounded by Alps, compared to the situation in Avignon, which is known for strong northern winds following the Rhone Valley towards the Mediterranean Sea.

Furthermore, the area of the intersection between inbound and outbound watershed is relatively more important for the site of Milan than for the site of Avignon, accounting for 19.4% and 15.5% of the combined in- and out-bound windshed area, respectively. The intersection of windsheds is particularly interesting in biogeographical terms as it constitutes an area where airborne communities from both the in- and the out-bound windsheds are present.

* Data retrieved from http://matthewkling.net/shiny/windscape/

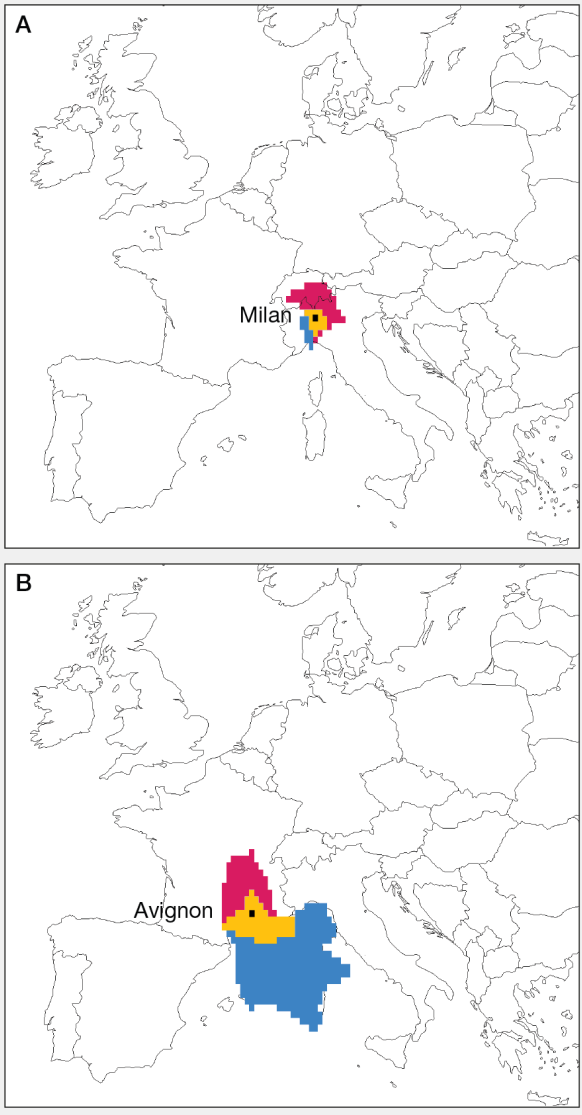

Figure 14.1. Windsheds computed via the model by Kling and Ackerly (2020) (http://matthewkling.net/shiny/windscape/) for (**A**) Milan, Italy and (**B**) Avignon, France. In both cases, the inbound windshed is indicated in red, the outbound one in blue, and the intersection of the two windsheds in yellow.

definition and delimitation of atmospheric biogeographic regions, and it has already been applied in the context of plant disease surveillance. For example, Meyer *et al.* (2017a) proposed the concept of *airborne catchment area* to delineate geographic regions from which airborne spores of wheat stem rust can be transported to a target location in Ethiopia where a new race of the pathogen was first detected in August 2012. To narrow down the possible source locations, they restricted the study to only the wheat-producing regions around Ethiopia and considered the times of the year in which the wheat season in Ethiopia and at the source location overlap.

⏩ Applications of biogeography to plant disease surveillance

Biogeographical studies have long recognized the impact of long-distance air dispersal in shaping the biogeography of plant pathogens. Summerell *et al.* (2010), for instance, identified the three main causes of long-range movements of *Fusarium*, a globally spread genus of fungi that includes several plant pathogens: air dispersal, soil spread and human-assisted movement of contaminated host plants. The biogeography of this genus is closely related to its phylogeography, with different *Fusarium* species displaying distinct geographical patterns, ranging from cosmopolitan (mostly air-dispersed) to regional (climate- or host-mediated; Summerell *et al.*, 2010). Similarly, Dietzel *et al.* (2019) discovered that the most ubiquitous fungal pathogens species found in dust samples across the United States are airborne, opportunistic and adaptable to stress. The regionalization of species-specific patterns may be attributed to spore traits that affect their dispersal and survival in the environment. In the particular case of airborne dispersal, Wang *et al*. (2021) tested the effect of fungal spore traits in their dispersal abilities. The study revealed that both aerodynamic (e.g., size, diameter, shape, density) and non-aerodynamic (e.g., diel vs. seasonal timing of spore release, longevity, source) factors influence the risk of arrival of spores in Australia. The researchers identified generalized spatio-temporal dynamics of fungal dispersal patterns that apply to all species sharing common spore traits, reducing the need for direct field observations.

Other studies have examined the dispersal of specific plant pathogens, focusing on surveillance from a biogeographic perspective. For example, Schmale *et al.* (2006) analyzed the genetic structure of atmospheric populations of *Gibberella zeae*, the causal agent of Fusarium head blight of wheat and barley, as well as Gibberella ear rot of corn. Their research revealed limited diversity across Northern United States, indicating significant genetic exchange among populations originating from various locations and being further mixed through aerial spread. The researchers conclude that local management practices may not be effective in reducing the risk of infection, as inoculum can be transported from distant areas.

⏩ Atmospheric dissemination of plant pathogens as epidemic networks

Networks are key concepts in epidemiology: they are mathematical objects composed of nodes (fixed elements) connected via edges, representing relations between nodes (Newman, 2003). They can be used to describe the way and frequency at which susceptible hosts are connected, and hence they can be used to predict the fate of an epidemic within a metapopulation of hosts. In fact, in the case of epidemiological networks,

nodes represent hosts (or groups of them) and edges represent potential transmission events of the disease (Jeger *et al.*, 2007). The topological structure of the constructed network can then be used to infer key characteristics of the host population, such as the identification of hot-spots of epidemic emergence, the presence of spreaders (Paull *et al.*, 2012), or features of the epidemic itself, such as the basic reproductive number (Colizza and Vespignani, 2008; Holme and Masuda, 2015).

For the particular case of airborne plant pathogens, the connectivity structure emerging from air-mass movement (e.g., trajectories or plumes) critically depends on key epidemiological and biophysical parameters, affecting the long-distance dispersal of pathogens (Figure 14.2). Aylor (2017) distinguishes between:
– Release from the leaf/stem/fruit,
– Canopy escape,
– Dispersal and survival in the atmosphere,
– Deposition over a susceptible host,
– Infection and establishment of the disease.

Aerobiological details about the entire dispersal process are outlined in Box 14.2: Airborne dispersal of plant pathogens. From a modelling perspective, phases A-B and D serve as the boundary conditions for simulating the aerial transport of pathogens, which is the initial step for constructing connectivity networks.

Box 14.2. Airborne dispersal of plant pathogens

The probability of host infection is proportional to the number of spores released (phase A), which is primarily affected by the severity of the disease and on biological and environmental factors that impact the process of sporulation. It is important to differentiate between actively released (liberated in the atmosphere by an active mechanism) and passively released spores (Levetin, 2015). The latter are more common and include spores whose discharge in the atmosphere is due to environmental drivers, such as wind, raindrops or rain splash, which break the electrostatic bonds holding the spores to the parent mycelium. The canopy (B) acts as a first barrier to airborne dispersal, as most spores are typically deposited within the crop itself. It is represented by barriers (leaves, branches, stems), sheltering from atmospheric agents such as turbulence or rain. Atmospheric dispersal (C) determines how pathogens spread geographically. Once a pathogen reaches the free troposphere, above the planetary boundary layer (PBL), its fate is determined by its aerodynamic properties, protection against harmful atmospheric conditions, and the atmospheric conditions themselves. The aerodynamic diameter determines the lifetime of the pathogen in the atmosphere: smaller particles are dispersed in turbulent conditions and are rarely deposited by gravity. Harmful environmental conditions, such low temperatures, rain washout, and UV affect dramatically the viability of spores (Levetin, 2015). Thin-walled spores, without protection, can survive for a few hours under sunlight, longer during nighttime or cloudy weather (Oneto *et al.*, 2020). Moreover, the concentration of viable spores in the atmosphere decreases with increased atmospheric turbulence (Aylor, 2017). Deposition (D) completes the transfer of inoculum on a susceptible host. It can be either dry (due to gravity) or wet (due to rain; Aylor, 2017). Wet deposition provides suitable environmental conditions for infection (Nagarajan and Singh, 1990; Roelfs *et al.*, 1992). If the spores are deposited on a susceptible host with favorable environmental conditions, an infection occurs (E).

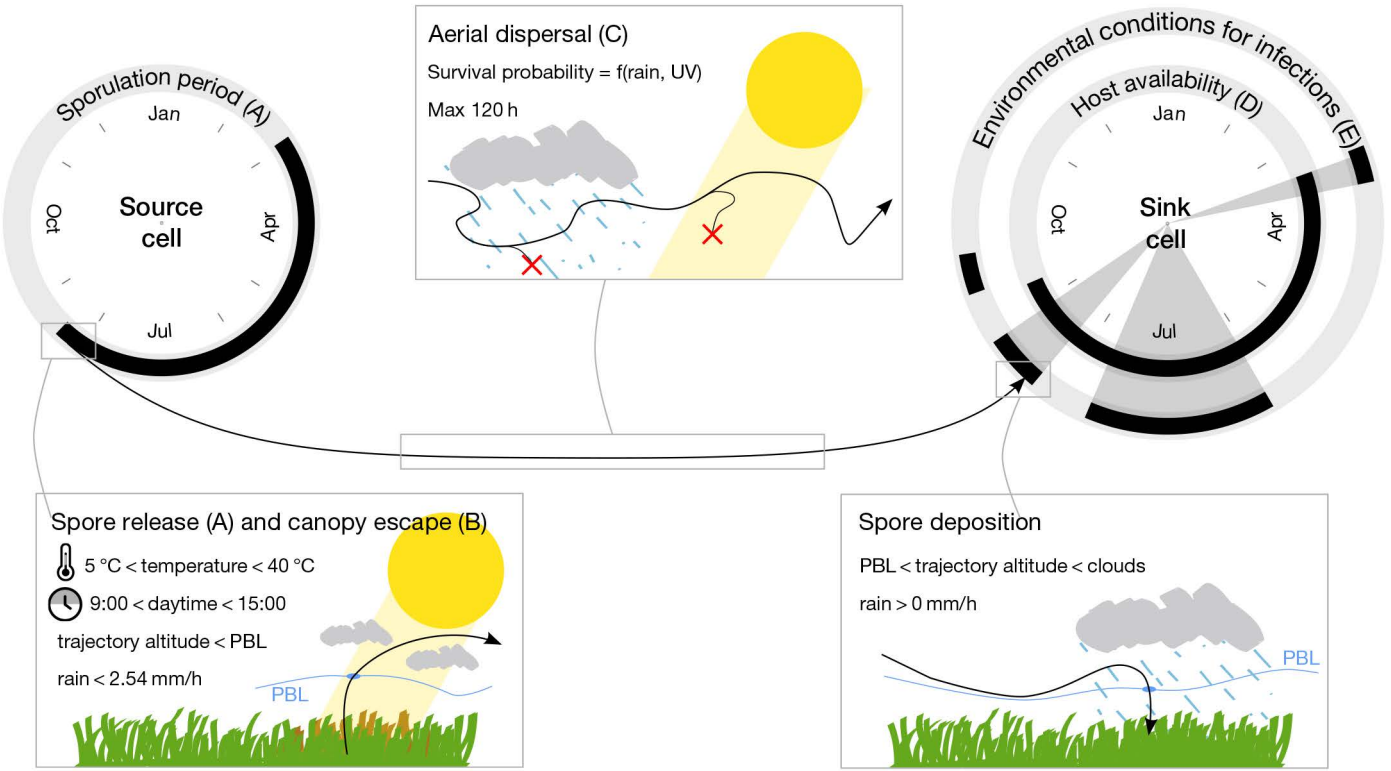

Figure 14.2. Schematic representation of the phases of the aerial transport of *Puccinia graminis*, causal agent of stem rust of wheat.

Infected plants release spores during sporulation (**A**); in this case, this occurs when specific environmental conditions (temperature, rain) are satisfied and in presence of turbulence (here assumed during daylight hours) that allow the spores to escape the canopy (**B**) and to reach the uppermost section of the atmosphere, over the PBL where winds are less turbulent and spores can travel further. During dispersal (**C**), spores must endure harsh environmental conditions, such as exposure to UV radiation. Rain can wash out spores below the base of the clouds and deposit them on susceptible hosts (**D**). If favorable conditions are met after deposition (E) an infection will be triggered (adapted from Radici *et al.*, 2022). PBL, Planetary Boundary Layer.

A classic approach to mathematically describe the dispersal of bio-particulates in the atmosphere, such as the Gaussian puff model that was originally conceived to study the impact of pollutant gases (Beychok, 1979), was based on strong simplifications of atmospheric dynamics (constant wind, no obstacles, uniform atmosphere, no particulates deposition). The Gaussian puff model belongs to the Eulerian approach, in opposition to the Lagrangian one. These terms refer to different perspectives of the observer in analyzing fluid motions: the former assumes the observer has a static reference point and observe the fluid move while the latter move in solidarity with the fluid particles themselves. The mathematical formalism that distinguish these approaches in transport modeling is described in detail in Chapter 4. Recent research in atmospheric transport of plant pathogens has moved in the direction of Lagrangian models (Gilligan, 2024). One example of these models is the Lagrangian trajectory model, which aims to study the deterministic trajectory of each released particle by means of simulations (Figure 14.2A) based on the three-dimensional wind velocity field $v = (v_x, v_y, v_z)$ in each point $x(t)$, $y(t)$, $z(t)$ and time t at each instant defined by the time step Δt (Equation 14.1):

$$x(t + \Delta t) \approx x(t) + \Delta t\, v_x(x(t), y(t), z(t), t)$$
$$y(t + \Delta t) \approx y(t) + \Delta t\, v_y(x(t), y(t), z(t), t)$$
$$z(t + \Delta t) \approx z(t) + \Delta t\, v_z(x(t), y(t), z(t), t)$$

Lagrangian models can be refined into Lagrangian dispersion models or more complex models, such as HYSPLIT (Draxler and Hess, 1998) or NAME (Jones and Harrison, 2004). These models integrate advection (the regular bulk motion) with diffusion (the casual motion due to turbulence) of particles in a fluid and are widely used to model wind-driven dispersal of biological particulates, from pollens (Bogawski *et al.*, 2019) to plant pathogens (Meyer *et al.*, 2017a, 2017b; Prank *et al.*, 2019; Radici *et al.*, 2022; Wang *et al.*, 2021). Moreover, most of these models allow for simulating the survival of spores to harmful atmospheric agents: mortality by drought (cumulative UV radiation), by freezing (low temperature), rain washout and gravitational deposition by integrating an enormous amount of weather data and reanalysis (Rodell *et al.*, 2004).

Lagrangian dispersal models are already in use to support early warning systems, like the one proposed by Allen-Sader *et al.* (2019). It relies on dispersal simulations to forecast the incidence of wheat rust diseases, inform agricultural advisors and guide control measures. The early warning system is currently active in Ethiopia and, since 2022, it has also been implemented in Nepal and Bangladesh (Smith *et al.*, 2024).

The advantage of Lagrangian trajectories models is that they are simple enough to provide as output a tridimensional trajectory, defined by the integration of the systems of Equation 14.1, from multiple release sites to multiple deposition sites. This information can be stored in a connectivity matrix (Box 14.3), representing a network.

In the construction of an airborne connectivity network, the structure of the edges is shaped by airborne dispersal of pathogens between distant hosts. This, in turn, defines the properties of the network itself. In network science, networks are categorized as undirected or directed (where a node is connected to another, but not necessarily vice versa); simple (where nodes are either connected or unconnected) or weighted (where edges are assigned a continuous value representing the strength of the link). Networks are commonly represented in terms of matrices, whose rows and columns

represent the nodes of the network, and whose non-null elements identify the presence of a connection. For airborne connectivity networks, nodes represent the sites of release or deposition Figure 14.3A-C), while an edge from a node *i* to another node *j* represents the intersection of a trajectory released in site *i* with site *j* (Choufany *et al.*, 2021; Meyer *et al.*, 2017b; Radici *et al.*, 2024). Eventually, an edge may represent not just the presence of a connection between *i* and *j*, but rather the frequency of the connections, which determines the strength of the connection (Figure 14.3D). In this case, the connectivity network is represented as a weighted matrix. An example of software that computes Lagrangian air mass trajectories with HYSPLIT to automatically produce weighted connectivity networks is Tropolink (Richard *et al.*, 2023).

⏩ Applications of airborne connectivity networks to plant disease surveillance

Epidemiological networks foster the use of network properties to develop and simulate surveillance strategies. Network-based surveillance involves the idea of prioritizing nodes, *i.e.* of hosts (or groups of hosts sharing the same location), to be monitored regularly, looking for signs of disease (Holme, 2018). This prioritization, which is based on network topology, is necessary because monitoring a crop is expensive.

Models of the spread of airborne plant diseases are relatively new, as most research on this topic relies on computationally intensive Lagrangian models (like HYSPLIT and NAME). This is why network-based surveillance studies of airborne diseases are

Box 14.3. From Lagrangian trajectories to networks

Spore dispersal can be represented as a 3D Lagrangian trajectory starting from a release site (source) where infectious hosts are present (Figure 14.3). We consider a simple case in which the trajectory is deterministic, *i.e.* we neglect the effect of turbulence and vertical wind-shear. The domain of this transport event consists of square cells ($0.5° \times 0.5°$) covered with wheat (the darker, the densest) from the Map Spam database*. (A) a 3D Lagrangian trajectory simulation is traced using HYSPLIT** from the source (cell 3034) in a given time and for a given duration. Its 2D projection on the Earth's surface intersects other cells; however, (B) cells intersected in which no deposition event occurs (due to various reasons, specified in Figure 14.3) are eliminated. In this case, cells without hosts are also excluded, since we are interested in identifying potential infections. In (C), cells likely to be deposition sites (sinks) are selected, and the trajectory is converted into a directed graph, with edges connecting the source to the sinks. Using network formalism, (D) epidemic connections from the source are represented as a row in an adjacency matrix. By repeating the simulations for each possible source in the domain and for each release date within a study period, a weighted matrix can be obtained, in which each element corresponds to the frequency of connections between nodes. It is important to note that repeating the simulations multiple times partially compensates for neglecting stochastic components in the deterministic trajectories. Both the adjacency and weighted matrices are referred to as connectivity matrices, since their edges signify connections among nodes.

* https://mapspam.info/

** https://www.ready.noaa.gov/HYSPLIT.php

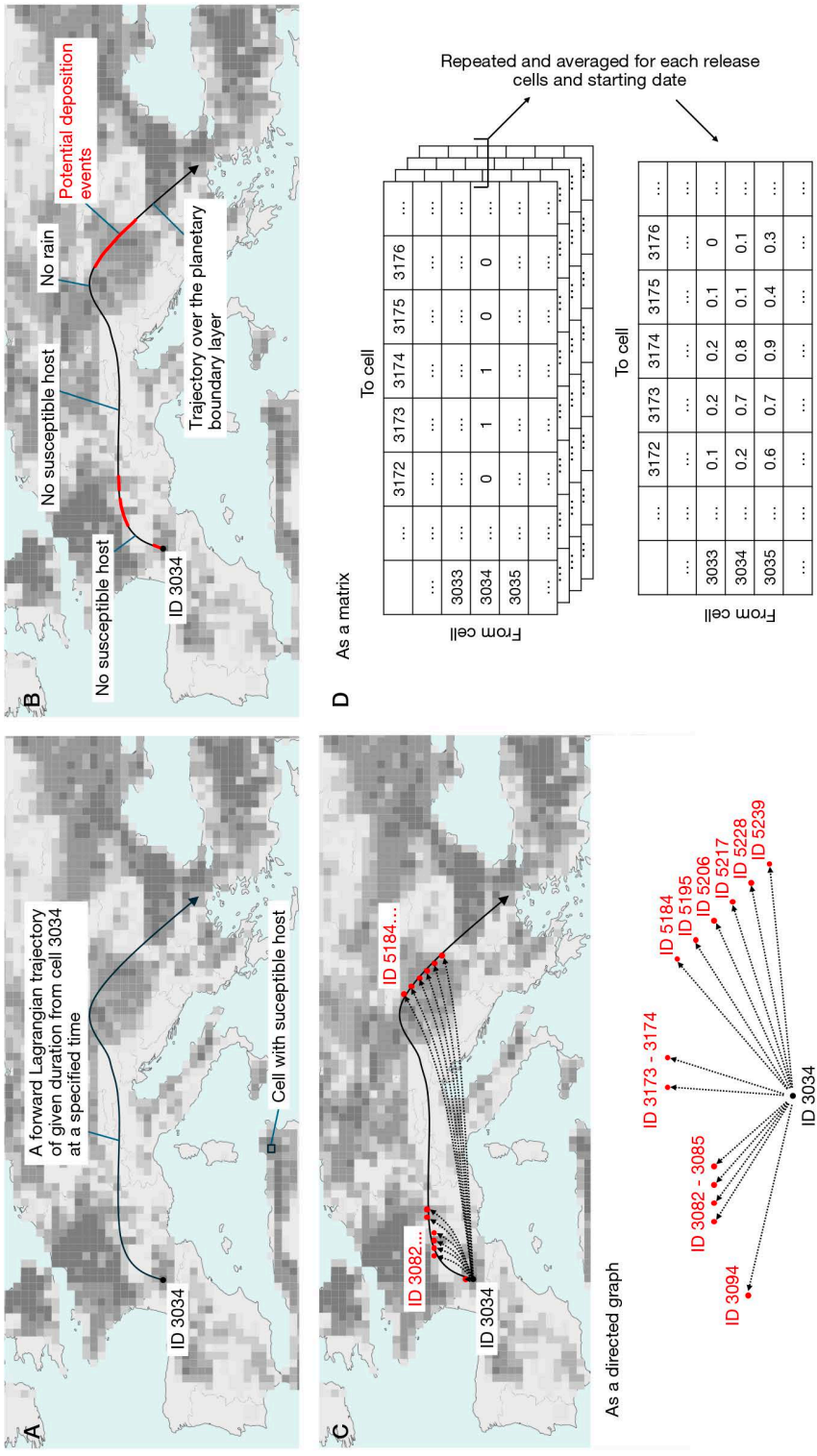

Figure 14.3. From a modelled transport event to its representation as a contact network.

(**A**) A tridimensional Lagrangian trajectory is traced from cell 3034 (source) in a given time and for a given duration; (**B**) only cells crossed by the trajectory where deposition event could have occurred (sinks) are retained; (**C**) the trajectory between the source and possible sinks is transformed into a directed graph; (**D**) epidemic connections from cell 3034 are represented as a row of a matrix; a weighted matrix is obtained by repeating the simulations for each source and for each release date.

innovative and pioneering (Jeger *et al.*, 2007). A groundbreaking study was conducted by Sutrave *et al.* (2012), who modelled the aerial spread of soybean rust among U.S. counties (nodes). The intensity of edges between nodes depend on geographic distance, prevailing wind strength and direction (weighted, directed edges).

There are various indicators that help identify the most important nodes (Newman, 2003). For example, the degree of a node is the number of nodes connected to it. Intuitively, the higher the degree, the more epidemiologically important a node is. In the case of directed networks, one can distinguish between out-degree (the number of nodes pointed to by a node) or in-degree (the number of nodes pointing to the node itself). In the case of weighted networks, the concept of degree may evolve into that of strength: rather than counting edges, the in/out-strength measure the total weight associated to the in/out going edges. For instance, Meyer *et al.* (2017b), who used NAME to investigate continental dispersal of *Puccinia* spores, used the ratio between out-strength and the total strength to identify donor and receptor countries. Sutrave *et al.* (2012) suggested that a surveillance strategy mixing node strength and past infection frequency of the nodes outperforms a strategy based on past infection frequency alone.

Network scientists have recently developed more complex indicators to identify the nodes that may play an important role in spreading a disease (De Arruda *et al.*, 2014; Jeger *et al.*, 2007). These indicators often take into consideration not only the local importance of a node (such as the degree, which consider a node and its immediate surroundings) but rather its role with respect to the whole network (Latora and Marchiori, 2007). These methods are usually more computational expensive, but provide better results compared to most elementary indicators, since they mimic the spatiotemporal spread of a disease. Nevertheless, these indicators have been the subject of study primarily outside the context of plant epidemiology, and their application to the case of airborne dispersal remains mostly unexplored.

⏩ Lagrangian trajectories and network formalism to investigate the scale of surveillance

There is growing evidence that airborne dispersal facilitates the introduction or re-introduction of new plant diseases into territories located thousands of kilometers away. For instance, a study based on HYSPLIT simulations corroborated the idea that hurricane Ivan led to the introduction of soybean rust in the US by dragging *Phakopsora pachyrhizi* over the Caribbeans from Colombia (Isard *et al.*, 2005), while a recent study compared spore dispersal simulation (using NAME) and genetic analysis of urediospores in South Africa and Australia suggesting that the periodic introduction of rust pathogens into Australia may be due to airborne transport of spores released in South Africa (Visser *et al.*, 2019).

This increasing evidence of the potential scale of airborne pathogen transport has heightened international concern about the risk of new introductions causing unforeseen production losses (Corredor-Moreno and Saunders, 2020; Ristaino *et al.*, 2021; Saunders *et al.*, 2019). Motivated by this risk, policymakers, scientists and stakeholders are re-considering plant protection measures against long-distance dispersed pathogens and are moving towards shared surveillance systems (Carvajal-Yepes *et al.*, 2019; Park *et al.*, 2011; see also note 10).

Despite the evidence showing the need to transition from an inefficient plant disease management based on political boundaries (Thompson *et al.*, 2016), there have been few attempts to quantify the benefits of an international cooperative surveillance system for transboundary diseases, *i.e.* those infectious diseases whose rapid spatial spread is likely to concern more than a country (Radici *et al.*, 2023). In the following paragraphs, we will present our attempt to address this question by using Lagrangian trajectory simulations and network properties.

In Radici *et al.* (2022), we studied the global transport of *P. graminis* spores and represented it as a network. We used a Lagrangian modelling framework as outlined in the previous sections of the chapter. Firstly, we identified areas worldwide with dense wheat cultivation; divided them in square cells (~2,000 km²) and ran Lagrangian trajectory simulations to mimic airborne transport (Figure 14.4A). By applying filtering criteria over the trajectories, we identified connections among cells, as summarized in Figure 14.3. We repeated these simulations for each cell, using crop calendars in the period 2013-2018. Finally, we formalized the connections as a matrix (Figure 14.3C and D). The resulting connectivity network (Figure 14.4A) exhibited high edge density, revealing both strong regional clusters and rare –but extremely long– dispersal events.

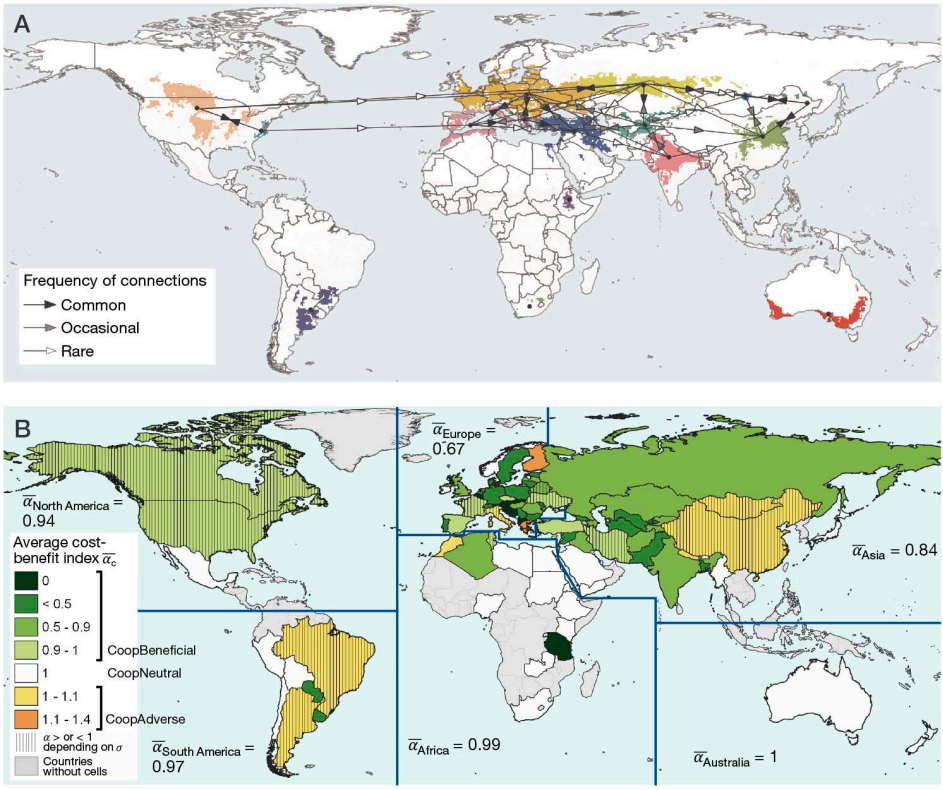

Figure 14.4. The global connectivity network (nodes more densely connected are represented with the same color) representing potential *Puccinia* transport events (**A**; Radici *et al.*, 2022) and the map of the average cost-benefit index α (**B**) by country in which also average values by continents, weighted by country wheat production 2010-2020, are displayed (Radici *et al.*, 2023).

For the purpose of developing a network-based surveillance system, we tested a new node ranking algorithm, called the Set cover. This algorithm iteratively selects a node of the network (a sentinel) which monitors the largest set of unmonitored nodes until all nodes are either sentinels or monitored. The cardinality of the set of sentinels is a proxy of the effort needed to monitor a given set of nodes, and so of the cost of surveillance.

In Radici *et al.* (2023), we compared the efficiency of the surveillance system under two scenarios. In the first, the network is treated as a whole ("coop"). In the second, it is artificially divided into separated subnetworks, representing each country ("non-coop"). This division allows the impact of transboundary connections to be assessed, which are removed in the "non-cooperative" scenario. For each country, we computed a cost benefit index α, i.e., the ratio between the average surveillance effort in the "coop" and the "non-coop" scenario for monitoring the same number of nodes.

The geographical distribution of α allows us to (i) compute the global advantage of a "coop" surveillance strategy over a "non-coop" one and (ii) identify which countries would benefit the most from cooperation (Figure 14.4B). Out of the 87 main wheat producing countries, 63% benefit from cooperation, as they need less sentinels in the coop scenario on average ("CoopBeneficial" in Figure 14.4B). Only 10% of the countries would have a cost ("CoopAdverse"), meaning that they would need to deploy a higher surveillance effort than they would put in place if they surveyed only in their own interest.

⏩ Conclusions and perspectives

In this chapter we discussed how we can leverage biogeographic and network concepts to inform surveillance strategies more effectively.

We demonstrated how biogeography concepts and tools are increasingly being used to investigate patterns of atmospheric microbial distribution and how recent research has linked the biogeography of pathogens to plant surveillance. Additionally, we introduced the concept of *windshed*, which provides new analytical instruments to characterize spatial diversity of airborne microbial communities.

Furthermore, we explained how to build connectivity networks starting from Lagrangian trajectory simulations of airborne dispersal of pathogens. Network-based methods help identifying those nodes (sites/hosts) that play crucial epidemiological roles in the spread of airborne pathogens, and which should be monitored systematically to provide valuable insights into disease presence.

Lastly, we presented a case study in which Lagrangian trajectories and networks were used to design a global surveillance strategy. Due to the large dispersal scale of airborne pathogens, an internationally shared surveillance strategy proves to be more effective than a country specific approach. However, some countries may need to increase their effort in the global interest, necessitating a mechanism of burden sharing.

As modelling approaches become more and more available, it is now time to revisit the empirical evidence of atmospheric biogeography and dissemination patterns. With the exception of a study by Visser *et al.* (2019), that confirmed the close relationship between South African and Australian samples of *P. graminis* by combining genetic analysis and atmospheric dispersal modelling, very few studies used field observations

to confirm biogeographical patterns or long-distance dissemination of plant pathogens. Future advances in this area will involve setting up experiments to demonstrate the suitability of these innovative modelling approaches for predicting the behavior of more airborne plant pathogens in the atmosphere with sufficient accuracy. This will allow for a wider use in designing better epidemic surveillance strategies.

Literature cited

Allen-Sader C., *et al*., 2019. An early warning system to predict and mitigate wheat rust diseases in Ethiopia. *Environ. Res. Lett.*, 14 (11), 115004. https://doi.org/10.1088/1748-9326/ab4034

Archer S., *et al*., 2022. Global biogeography of atmospheric microorganisms reflects diverse recruitment and environmental filtering. *Research Square*. https://doi.org/10.21203/rs.3.rs-244923/v4

Aylor D.E., 2017. *Aerial dispersal of pollen and spores*, APS Press, St. Paul, MN, 418 p. https://doi.org/10.1094/9780890545430

Barberán A., *et al*., 2015. Continental-scale distributions of dust-associated bacteria and fungi. *Proc. Natl Acad. Sci. USA*, 112 (18), 5756-5761. https://doi.org/10.1073/pnas.1420815112

Bertolini V., *et al*., 2013. Temporal variability and effect of environmental variables on airborne bacterial communities in an urban area of Northern Italy, *Appl. Microbiol. Biotechnol.*, 97 (14), 6561-6570. https://doi.org/10.1007/s00253-012-4450-0

Beychok M.R., 1979. *Fundamentals of stack gas dispersion*, Open Library, M.R. Beychok, Newport Beach, Calif., 201 p.

Bogawski P., *et al*., 2019. Detecting distant sources of airborne pollen for Poland: Integrating back-trajectory and dispersion modelling with a satellite-based phenology. *Sci. Tot. Environ*, 689, 109-125. https://doi.org/10.1016/j.scitotenv.2019.06.348

Bowers R.M., *et al*., 2013. Seasonal variability in bacterial and fungal diversity of the near-surface atmosphere. *Environ. Sci. Technol.*, 47 (21), 12097-12106. https://doi.org/10.1021/es402970s

Brodie E.L., *et al*., 2007. Urban aerosols harbor diverse and dynamic bacterial populations. *Proc. Natl. Acad. Sci. USA*, 104 (1), 299-304. https://doi.org/10.1073/pnas.0608255104

Brown J.K.M., Hovmøll M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science*, 297 (5581), 537-541. https://doi.org/10.1126/science.1072678

Bryde R.L.W., Willets H.J., 1977. The brown rot fungi of fruit. Their biology and control. Elsevier, 171 p. https://doi.org/10.1016/C2013-0-02715-6

Burrows S.M., *et al*., 2009. Bacteria in the global atmosphere – Part 1: Review and synthesis of literature data for different ecosystems. *Atmos. Chem. Phys.*, 9 (23), 9263-9280. https://doi.org/10.5194/acp-9-9263-2009

Cáliz J., *et al*., 2018. A long-term survey unveils strong seasonal patterns in the airborne microbiome coupled to general and regional atmospheric circulations. *Proc. Natl Acad. Sci. USA*, 115 (48), 12229-12234. https://doi.org/10.1073/pnas.1812826115

Carvajal-Yepes M., *et al*., 2019. A global surveillance system for crop diseases. *Science*, 364 (6447), 1237-1240. https://doi.org/10.1126/science.aaw1572

Choufany M., *et al*., 2021. Inferring long-distance connectivity shaped by air-mass movement for improved experimental design in aerobiology. *Sci. Rep.*, 11 (1), 1-10. https://doi.org/10.1038/s41598-021-90733-2

Colizza V., Vespignani A., 2008. Epidemic modeling in metapopulation systems with heterogeneous coupling pattern: Theory and simulations. *J. Theor. Biol.*, 251 (3), 450-467. https://doi.org/10.1016/j.jtbi.2007.11.028

Corredor-Moreno P., Saunders D.G.O., 2020. Expecting the unexpected: Factors influencing the emergence of fungal and oomycete plant pathogens. *New Phytol*, 225 (1), 118-125. https://doi.org/10.1111/nph.16007

De Arruda G.F., *et al*., 2014. Role of centrality for the identification of influential spreaders in complex networks. *Physical Review E – Statistical, Nonlinear, and Soft Matter Physics*, 90 (3), 1-17. https://doi.org/10.1103/PhysRevE.90.032812

Dietzel K., *et al.*, 2019. Geographical distribution of fungal plant pathogens in dust across the United States. *Front. Ecol. Evol.*, 7. https://doi.org/10.3389/fevo.2019.00304

Draxler R.R., Hess G.D., 1998. An overview of the HYSPLIT_4 modelling system for trajectories, dispersion and deposition. *Australian Meteorological Magazine*, 47 (4), 295-308.

Fierer N., *et al.*, 2008. Short-term temporal variability in airborne bacterial and fungal populations. *Appl. Environ. Microbiol.*, 74 (1), 200-207. https://doi.org/10.1128/AEM.01467-07

Fröhlich-Nowoisky J., *et al.*, 2009. High diversity of fungi in air particulate matter. *Proc. Natl Acad. Sci. USA*, 106 (31), 12814-12819. https://doi.org/10.1073/pnas.0811003106

Fröhlich-Nowoisky J., *et al.*, 2012. Biogeography in the air: Fungal diversity over land and oceans. *Biogeosciences*, 9 (3), 1125-1136. https://doi.org/10.5194/bg-9-1125-2012

Gilligan C.A., 2024. Developing predictive models and early warning systems for invading pathogens: Wheat rusts. *Annu. Rev. Phytopathol.*, 62: 217-241. https://doi.org/10.1146/annurev-phyto-121423-041956

Gusareva E.S., *et al.*, 2019. Microbial communities in the tropical air ecosystem follow a precise diel cycle. *Proc. Natl Acad. Sci. USA*, 116 (46), 23299-23308. https://doi.org/10.1073/pnas.1908493116

Holme P., Masuda N., 2015. The basic reproduction number as a predictor for epidemic outbreaks in temporal networks. *PLOS ONE*, 10 (3), e0120567. https://doi.org/10.1371/journal.pone.0120567

Holme P., 2018. Objective measures for sentinel surveillance in network epidemiology. *Phys. Rev. E*, 98 (2), 1-11. https://doi.org/10.1103/PhysRevE.98.022313

Isard S.A., *et al.*, 2005. Principles of the atmospheric pathway for invasive species applied to soybean rust. *BioScience*, 55 (10), 851-861. https://doi.org/10.1641/0006-3568(2005)055[0851:POTAPF]2.0.CO;2

Jeger M.J., *et al.*, 2007. Modelling disease spread and control in networks: Implications for plant sciences. *New Phytol*, 174, 279-297. https://doi.org/10.1111/j.1469-8137.2007.02028.x

Jones A.M., Harrison R.M., 2004. The effects of meteorological factors on atmospheric bioaerosol concentrations — a review. *Sci. Tot. Environ.*, 326, 151-180. https://doi.org/10.1016/j.scitotenv.2003.11.021

Kling M.M., Ackerly D.D., 2020. Global wind patterns and the vulnerability of wind-dispersed species to climate change. *Nat. Clim. Change*, 10 (9), 868-875. https://doi.org/10.1038/s41558-020-0848-3

Kling M.M., Ackerly D.D., 2021. Global wind patterns shape genetic differentiation, asymmetric gene flow, and genetic diversity in trees. *Proc. Natl Acad. Sci. USA*, 118 (17), e2017317118. https://doi.org/10.1073/pnas.2017317118

Latora V., Marchiori M., 2007. A measure of centrality based on network efficiency. *New J. Phys.*, 9, 188. https://doi.org/10.1088/1367-2630/9/6/188

Levetin E., 2015. Aerobiology of agricultural pathogens. *In:* Yates M.V. *et al.* (eds), *Manual of environmental microbiology*, Wiley, 3.2.8. https://doi.org/10.1128/9781555818821.ch3.2.8

Mahaffee W.F., Stoll R., 2016. The Ebb and flow of airborne pathogens: Monitoring and use in disease management decisions. *Phytopathology*, 106 (5), 420-431. https://doi.org/10.1094/PHYTO-02-16-0060-RVW

Meyer M., *et al.*, 2017a. Large-scale atmospheric dispersal simulations identify likely airborne incursion routes of wheat stem rust into Ethiopia. *Phytopathology*, 107 (10), 1175-1186. https://doi.org/10.1094/PHYTO-01-17-0035-FI

Meyer M., *et al.*, 2017b. Quantifying airborne dispersal routes of pathogens over continents to safeguard global wheat supply. *Nature Plants*, 3 (10), 780-786. https://doi.org/10.1038/s41477-017-0017-5

Nagarajan S., Singh D.V., 1990. Long-distance dispersion of rust pathogen. *Annu. Rev. Phytopathol.*, 28, 139-153. https://doi.org/10.1146/annurev.py.28.090190.001035

Newman M.E.J., 2003. The structure and function of complex networks. *Siam Rev*, 45 (2), 167-256. https://doi.org/10.1137/S003614450342480

Oneto D.L., *et al.*, 2020. Timing of fungal spore release dictates survival during atmospheric transport. *Proc. Natl Acad. Sci. USA*, 117 (10), 5134-5143. https://doi.org/10.1073/pnas.1913752117

Park R., *et al.*, 2011. International surveillance of wheat rust pathogens: Progress and challenges. *Euphytica*, 179 (1), 109-117. https://doi.org/10.1007/s10681-011-0375-4

Parnell S., *et al.*, 2017. Surveillance to inform control of emerging plant diseases: An epidemiological perspective. *Annu. Rev. Phytopathol.*, 55, 591-610. https://doi.org/10.1146/annurev-phyto-080516-035334

Paull S.H., *et al.*, 2012. From superspreaders to disease hotspots: Linking transmission across hosts and space. *Front. Ecol. Environ.*, 10 (2), 75-82. https://doi.org/10.1890/110111

Prank M., *et al.*, 2019. Climate change impacts the spread potential of wheat stem rust, a significant crop disease. *Environ. Res. Lett.*, 14, 124053. https://doi.org/10.1088/1748-9326/ab57de

Radici A., *et al.*, 2022. Early-detection surveillance for stem rust of wheat: Insights from a global epidemic network based on airborne connectivity and host phenology. *Environ. Res. Lett.*, 17, 064045. https://doi.org/10.1088/1748-9326/ac73aa

Radici A., *et al.*, 2023. Global benefits and domestic costs of a cooperative surveillance strategy to control transboundary crop pathogens. *Plants People Planet*, 5 (6), 923-932. https://doi.org/10.1002/ppp3.10379

Radici A., *et al.*, 2024. A metapopulation framework integrating landscape heterogeneity to model an airborne plant pathogen: The case of brown rot of peach in France. *Agric. Ecosyst. Environ.*, 367, 108994. https://doi.org/10.1016/j.agee.2024.108994

Richard H., *et al.*, 2023. Computing geographical networks generated by air-mass movement. *GeoHealth*, 7 (10), e2023GH000885. https://doi.org/10.1029/2023GH000885

Ristaino J.B., *et al.*, 2021. The persistent threat of emerging plant disease pandemics to global food security. *Proc. Natl Acad. Sci. USA*, 118 (23), 1-9. https://doi.org/10.1073/pnas.2022239118

Rodell M., *et al.*, 2004. The global land data assimilation system. *Bull. Am. Meteorol. Soc.*, 85 (3), 381-394. https://doi.org/10.1175/BAMS-85-3-381

Roelfs A.P., *et al.*, 1992. *Rust diseases of wheat: Concepts and methods of disease management*, CIMMYT, Mexico, 81 p.

Saunders D.G.O., *et al.*, 2019. Tackling the re-emergence of wheat stem rust in Western Europe. *Commun. Biol.*, 2 (1), 9-11. https://doi.org/10.1038/s42003-019-0294-9

Schmale D.G., *et al.*, 2006. Genetic structure of atmospheric populations of *Gibberella zeae*. *Phytopathology*, 96 (9), 1021-1026. https://doi.org/10.1094/PHYTO-96-1021

Smith J.W., *et al.*, 2024. Advancing crop disease early warning in South Asia by complementing expert surveys with internet media scraping. *Clim. Resil. Sustain.*, 3 (3), e78. https://doi.org/10.1002/cli2.78

Sommeria-Klein G., *et al.*, 2021. Global drivers of eukaryotic plankton biogeography in the sunlit ocean. *Science*, 374 (6567), 594-599. https://doi.org/10.1126/science.abb3717

Summerell B.A., *et al.*, 2010. Biogeography and phylogeography of *Fusarium*: A review. *Fungal Diversity*, 44 (1), 3-13. https://doi.org/10.1007/s13225-010-0060-2

Sutrave S., *et al.*, 2012. Identifying highly connected counties compensates for resource limitations when evaluating national spread of an invasive pathogen. *PLoS ONE*, 7 (6), e37793. https://doi.org/10.1371/journal.pone.0037793

Thompson R.N., *et al.*, 2016. Management of invading pathogens should be informed by epidemiology rather than administrative boundaries. *Ecol. Modell.*, 324, 28-32. https://doi.org/10.1016/j.ecolmodel.2015.12.014

Tignat-Perrier R., *et al.*, 2020. Seasonal shift in airborne microbial communities. *Sci. Tot. Environ*, 716, 137129. https://doi.org/10.1016/j.scitotenv.2020.137129

Uetake J., *et al.*, 2020. Airborne bacteria confirm the pristine nature of the Southern Ocean boundary layer. *Proc. Natl Acad. Sci. USA*, 117 (24), 13275-13282. https://doi.org/10.1073/pnas.2000134117

Visser B., *et al.*, 2019. Microsatellite analysis and urediniospore dispersal simulations support the movement of *Puccinia graminis* f. sp. *tritici* from Southern Africa to Australia. *Phytopathology*, 109 (1), 133-144. https://doi.org/10.1094/PHYTO-04-18-0110-R

Wang M., *et al.*, 2021. A general trait-based modelling framework for revealing patterns of airborne fungal dispersal threats to agriculture and native flora. *New Phytol.*, 232 (3), 1506-1518. https://doi.org/10.1111/nph.17659

Womack A.M., *et al*., 2010. Biodiversity and biogeography of the atmosphere. *Philos. Trans. R. Soc. B Biol. Sci.*, 365 (1558), 3645-3653. https://doi.org/10.1098/rstb.2010.0283

Xing Y., *et al*., 2020. Global cropland connectivity: A risk factor for invasion and saturation by emerging pathogens and pests. *BioScience*, 70 (9), 744-758. https://doi.org/10.1093/biosci/biaa067

Yadav I.C., Devi N.L., 2017. Pesticides classification and its impact on human and environment, *In:* Ram C. *et al*., *Environmental science and engineering,* Volume 6 *Toxicology,* 140-158.

General Conclusion

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Mirages from sensible heat on the horizon of a hot desert, dandelion seeds taking loft buoyed by the fine hairs of their parachutes, plumes from bush fires, sea spray… –these are some of the visible examples of physics in action to make entrance ramps for biological particles onto the highways in the sky. Bolstered by the content of the chapters of this book, the reader can now readily create mental images of the multitude of potential trajectories and destinies of biological particles along these highways. Furthermore, the chapters of this book add tremendous color to the voyage in terms of the chemistry, physical stresses and bustle of the multitude of travelers that share these highways. The seemingly wispy sky where clouds float is charged with thousands of tons of insects, with the ash and volatilized carbon of entire forests and with the never-ending flux of microbial life.

Some of the most pressing questions about these trajectories in the sky concern their starting point: where are the most intense sources for emissions of different types of biological particles and what is the role of human activities in these emissions? As research advances toward answers to these questions, we will be confronted with the need to account for the influence of global changes. How will emissions and transport be altered by climate change? There is concern that the effects of climate change will likely modify transport pathways, especially if the Atlantic Meridional Overturning Circulation slows or stops. Likewise, climate change might lead to new sources of bioaerosols with, for example, the release of ancient particles as permafrost thaws and collapses. In face of potentially new sources and new trajectories, the reader is reminded that emissions and transport processes will, nevertheless, be based on the same principles of physics outlined in this book. Therefore, it is essential that scientists involved in aerobiology master and facilitate experimentation based on these principles, and push for understanding aerobiological dynamics on the Earth system scale. We encourage the reader to put the lessons in this book to work.

List of abbreviations

AAR: Aerosol atmospheric rivers
AQI: Air Quality Index
AVOCs: Anthropogenic volatile organic compounds
BC: Black carbon
BVOCs: Biogenic volatile organic compounds
CCN: Cloud condensation nuclei
CFU: Colony forming units
CoV: Coronaviruses
DAPI: 4',6-diamidino-2-phenylindole
DEC: Disjunct Eddy Covariance
DEM: Digital Elevation Model
DEPs: Diesel exhaust particles
EAWM: East Asian Winter Monsoon
EC: Eddy-covariance
EF: Enrichment factors (chapter7)
EFs: Emission factors (chapter 8)
FBL: Flight Boundary Layer
FLEXPART: FLEXible PARTicle
GISP2: Greenland Ice Sheet Project 2
HDM: House dust mites
HIV/AIDS: Human immunodeficiency virus/acquired immunodeficiency syndrome
HNA: High nucleic acid
HYSPLIT: Hybrid Single-Particle Lagrangian Integrated Trajectory
IBD: Isolation-by-Distance
INP: Ice nucleating particles
IPCC: Intergovernmental Panel on Climate Change
ITCZ: Inter-Tropical Convergence Zone
ITS: Internal Transcribed Spacer
LDD: Long-distance dispersal
LGM: Last Glacial Maximum
LIF: Laser/light induced fluorescence
LNA: Low nucleic acid
MERS: Middle East respiratory syndrome
MODIS: Moderate Resolution Imaging Spectroradiometer
MOST: Monin-Obukhov Similarity Theory
NADH: Nicotinamide adenine dinucleotide phosphate
NAME: Numerical Atmospheric-dispersion Modelling Environment

NDVI: Normalized Difference Vegetation Index
NGS: Next Generation Sequencing
NIR: Near Infra-Red
NMVOCs: Non-methane volatile organic compounds
NOAA: National Oceanographic and Atmospheric Administration
OTU: Operational Taxonomic Unit
PBAP: Primary biological aerosol particles
PBAs: Primary biological aerosols
PBL: Planetary Boundary Layer
PCR: Polymerase Chain Reaction
PLAnET: PLant-Atmosphere Epiphytic Transport
PM: Particulate matter
REA: Relaxed Eddy Accumulation
RH: Relative humidity
Rif: Richardson flux number
ROS: Reactive oxygen species
RV: Rhinoviruses
SARS: Severe acute respiratory syndrome
SSA: Sea spray aerosol
TB: Tuberculosis
UAS: Uncrewed aircraft systems
UFPs: Ultra-fine particles
UV-APS: Ultraviolet Aerodynamic Particle Sizer
VLR: Vertical Looking Radar
VOC: Volatile organic compounds
WAIS: West Antarctic Ice Sheet
WHO: World Health Organization
WWTP: Waste water treatment plants

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This book explores the atmosphere as a dynamic transport system for small biological particles in the atmosphere, with a focus on microorganisms and small insects, applicable to nematodes, spiders, tardigrades, etc. It brings together interdisciplinary competence from Life, Earth and Mathematical Sciences to describe emissions processes such as wildfire smoke, sea spray and recurrent uplift from plant canopies; transport processes and trajectories in the past, present and future; and how the voyagers survive the atmospheric physico-chemical conditions. The book introduces tools to trace dispersal routes, assess post-deposition impacts, as well as the concepts of "atmospheric biogeography" and "windsheds" to understand and anticipate microbial movement across landscapes and borders. It offers stimulus to both new and established researchers to undertake an important challenge in aerobiology: to more precisely characterize and quantify the dynamics of particle voyages on the highways of the atmosphere and identify the impacts of these voyages on disease epidemiology, environmental quality and the evolution of organisms.

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