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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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Table of contents

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.

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Section 1

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