

What goes up, must come down: air–soil microbiome connectivity and its implications for ecosystem functioning

Beatriz Sánchez-Parra^{1,2,*} & Nico Eisenhauer^{2,3}

¹Leipzig University, Institute of Biology, Biodiversity of the Atmosphere, Talstraße 33, D-04103, Leipzig, Germany

²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, D-04103, Leipzig, Germany

³Leipzig University, Institute of Biology, Puschstrasse 4, 04103, Leipzig, Germany

* Correspondence can be addressed to:

Jun.-Prof. Ph.D Beatriz Sánchez-Parra, Leipzig University, Institute of Biology, Biodiversity of the Atmosphere, Talstraße 33, D-04103, Leipzig, Germany

Tel.: +49 341 97 32911 Fax: +49 341 97 36789

Correspondence to: Beatriz Sánchez-Parra (beatriz.sanchez_parra@uni-leipzig.de)

Abstract

Soils harbor Earth's largest reservoir of microbial diversity, yet enormous numbers of microorganisms are continuously aerosolized, transported through the atmosphere, and redeposited across landscapes. Despite this pervasive exchange, soil and atmospheric microbiology have largely developed as separate disciplines. Here, we propose a conceptual framework that views soils and the atmosphere as a coupled microbiome linked by bidirectional microbial fluxes. We argue that the atmosphere is not merely a passive transport medium but a selective habitat that filters microbial communities during dispersal, while deposition and subsequent establishment further shape microbial assembly on the ground. This air–soil connectivity operates across local to intercontinental scales, linking microbial metacommunities and influencing biodiversity, ecosystem resilience, nutrient cycling, plant-microbiome assembly, pathogen dissemination, and climate feedback. Framing these interactions within a One Health perspective highlights their relevance for ecosystem management, agriculture, restoration, biosecurity, and public health. We identify key research priorities, including quantifying global microbial fluxes, determining colonization success, resolving the functional consequences of atmospheric dispersal, and integrating microbial transport into coupled Earth-system models. Recognizing the atmosphere and soils as an interconnected microbiome provides a new framework for understanding microbial biogeography and predicting ecosystem responses under accelerating global environmental change.

1. Introduction

The soil is a terrestrial ecosystem that contains a great diversity of microorganisms that constitute the soil microbiome. This microbiome allows essential ecosystem functions to take place such as N capture, C cycle, etc.... (Sokol et al., 2022). But the microorganisms of the edaphic microbiome are not static inside the soil, since they can be dispersed through the terrestrial ecosystem through other organisms, such as plants or soil fauna, and by aquatic ecosystems through water currents and dispersion by animals. Likewise, they can also reach the atmospheric ecosystem through aerosolization.

The atmosphere is a hostile ecosystem characterized by the scarcity of nutrients, the high exposure to UV light, desiccation, oxidation, and high temperature fluctuations. However, despite these hostile conditions, it also presents a diverse microbiome that, unlike that of other ecosystems, can be transported long distances, sometimes transoceanic, until it reaches a new ecosystem (Amato et al., 2023; Mayol et al., 2014, Kellogg and Griffin, 2006). Therefore, the atmospheric microbiome can act as a good connector of geographically separated ecosystems, also facilitating the exchange of microorganisms between terrestrial and aquatic environments.

Until now, the atmospheric microbiome has been analyzed as a separate microbiome from the rest, without taking into account that it comes from the microbiomes of the other ecosystems and that it then becomes part of them again when it is deposited. Therefore, we want to claim the connectivity that the atmospheric ecosystem exerts with the rest of ecosystems such as the soil. These microbiomes have traditionally been studied as independent compartments, yet they may be better understood as components of a connected soil-atmosphere microbiome continuum, in which microorganisms are not, by nature, unlimited, since selective filters exist during aerosolization, atmospheric transport itself and during microbial establishment after its deposition in the receiving ecosystem. But the interactions of these coupled microbiomes have a great influence on biodiversity, ecosystem functioning, and environmental health across scales (Figure 1).

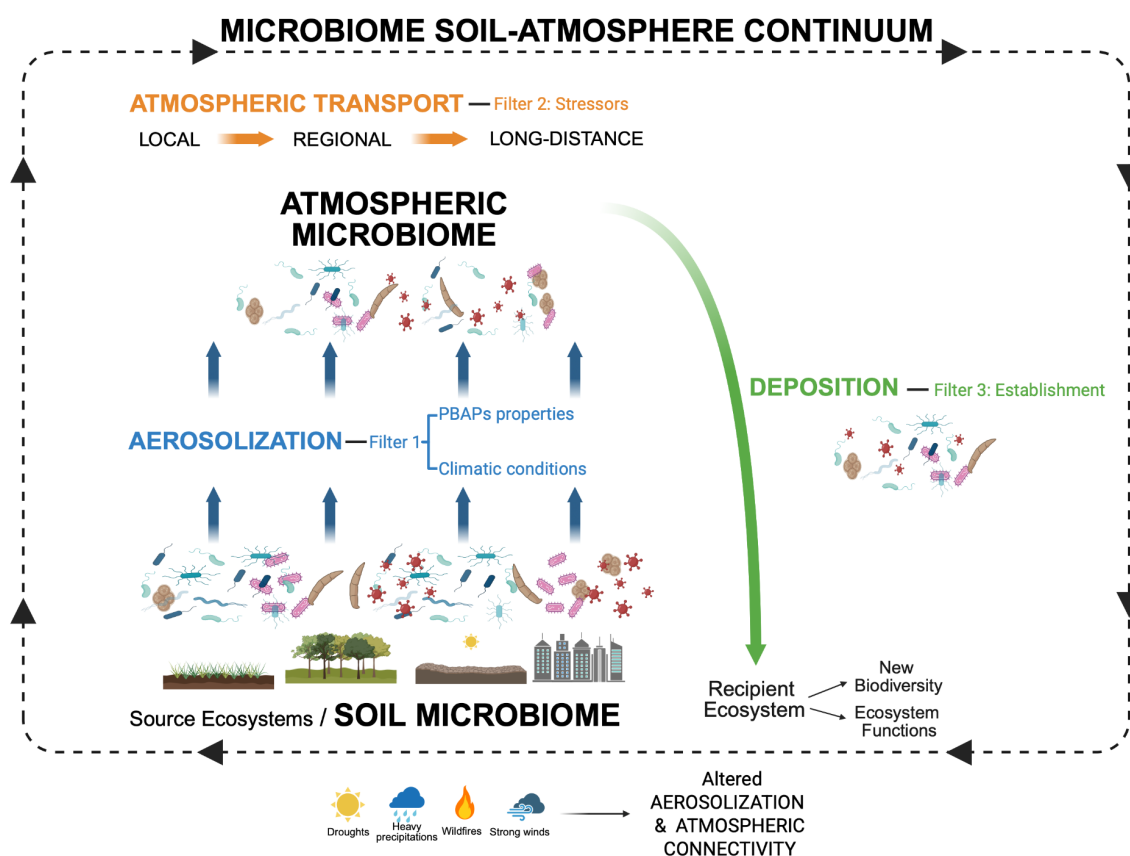


Figure 1: The soil-atmosphere microbiome continuum: connecting ecosystems across spatial scales. Microorganisms can be aerosolized from source ecosystems, enter the atmospheric microbiome, be transported at different scales and be deposited into recipient ecosystems where only a fraction may establish. In connectivity, there

are three main filters during aerosolization, atmospheric transport and deposition. Environmental disturbances can modify aerosolization and atmospheric connectivity. (Figure created at <https://BioRender.com>).

2. The bidirectional air–soil microbiome connection

2.1 Aerosolization: how soil microbes enter the atmosphere

Soil contains millions of microorganisms that can be aerosolized into the atmosphere. Those located in the uppermost soil layers are more likely to become aerosolized and reach the planetary boundary layer (PBL), the atmospheric layer closest to the surface (Morales-Baquero and Pérez-Martínez, 2016). Consequently, the PBL is expected to harbor a more dynamic and spatially heterogeneous atmospheric microbiome because it is the atmospheric layer closest to the Earth's surface and is directly influenced by surface forcings, such as frictional drag, evaporation, transpiration, or heat transfer (Sánchez-Parra et al., 2021). These interactions drive changes in atmospheric and surface conditions, including temperature, humidity, turbulence, and soil moisture, over relatively short timescales and across spatial scales. In addition, the productivity and type of terrestrial ecosystem underlying the PBL can influence the abundance and composition of microorganisms available for aerosolization. High-productivity ecosystems may provide a greater potential source of bioaerosols, while different land-cover types, such as forests, agricultural areas, wetlands, and coastal environments, can generate distinct bioaerosol profiles. Consequently, both temporal variation in surface conditions and spatial variation in ecosystem characteristics can alter the availability and aerosolization of resident microorganisms, contributing to variation in the composition and dynamics of the PBL microbiome (Stull, 1988; Emeis, 2013; Šantl-Temkiv et al., 2022).

Regarding the aerosolization process, various natural mechanisms come into play, such as the wind erosion which can entrain particles from the ground into the atmosphere (Acosta-Martínez et al., 2015), or raindrop splash, where a falling drop causes microorganisms in the immediate vicinity to disperse into the air (Joung et al., 2017; Bourouiba, 2021). Volcanic eruptions also serve as a natural mechanism that releases substantial quantities of microorganisms into the atmosphere (Griffin, 2021), often aerosolizing microorganisms from deeper soil layers than would otherwise occur. Furthermore, the atmospheric layers receiving microorganisms from volcanic eruptions are exposed to a highly specific microbiome, one resistant to the abiotic conditions characteristic of volcanoes and their surroundings, such as high temperatures and elevated sulfur content.

There are also anthropogenic mechanisms, such as agricultural tillage, harvesting, and other land-use activities, that can aerosolize microorganisms into the atmosphere. Agricultural and urban activities can substantially influence airborne biological loads and contribute to seasonal variation in the aerobiome (Lighthart, 1984; Poirier et al., 2026). The timing and environmental conditions under which these activities occur may further influence the quantity and composition of aerosolized microorganisms. For example, harvesting under dry soil conditions may promote the mechanical aerosolization of soil-associated microorganisms, whereas wetter conditions can alter particle mobilization and microbial release through different aerosolization mechanisms (Joung et al., 2017).

However, aerosolization also depends on the microorganisms themselves, specifically, their size (Deutscher Wetterdienst [DWD], n.d.), shape, and whether they possess structures that facilitate aerosolization. It also depends on whether the aerosolization process occurs passively or via active spore dispersal (Trail, 2007). Furthermore, their ability to withstand stressors such as

desiccation and UV radiation is significant, as is the development of protective structures or resistance mechanisms, such as sporulation or pigmentation (Tastassa et al., 2024).

Although microbial aerosolization may appear largely stochastic, it is influenced by the physical and biological characteristics of microorganisms, which determine their ability to become airborne and persist in the atmosphere. Microorganisms are more likely to be aerosolised and remain airborne when they possess traits that enhance their resistance to atmospheric stress. In particular, smaller microorganisms may remain suspended in the atmosphere for longer periods than larger ones (Tesson et al., 2016), while those capable of tolerating or developing defence mechanisms against environmental stress may have a greater likelihood of atmospheric persistence. Once released into the air, microorganisms enter an environment that differs markedly from their original habitat, such as soil, exposing them to a range of physical and chemical stressors.

Taken together, these processes indicate that environmental filtering begins before microorganisms become airborne, shaping the community that enters the atmosphere. Once airborne, microorganisms are then exposed to the distinct conditions of the atmosphere, which may further influence their persistence and fate.

2.2 The atmosphere as a microbial habitat

Microorganisms can be transported through the atmosphere over short or long distances (Fröhlich-Nowoisky et al., 2016) with long-range transport being facilitated when microorganisms are entrained into the free troposphere (Šantl-Temkiv et al., 2022). During the atmospheric transport, they encounter various stressors capable of causing damage, such as UV radiation, photooxidants, and atmospheric pollutants. They are also subjected to oxidative stress and drastic temperature changes, typically involving a drop in temperature as they ascend to the upper layers of the troposphere. In the lower troposphere, temperature also influences the short-range transport and suspension time of bioparticles by affecting their volatility. Studies have identified diurnal cycles for certain bacteria in this context: in the morning, as the sun rises and the air warms, bacteria are more likely to become aerosolized; conversely, at sunset, as near-ground temperatures drop, the bacteria settle back onto the surface (Gusareva et al., 2019). Other limiting factors include desiccation, water scarcity, and, more generally, nutrient limitation. All this demonstrates that the atmosphere is not merely a transport belt, but rather a hostile ecosystem where aerosolized bioparticles are affected.

However, some microorganisms have developed forms of resistance, such as spores, that allow them to withstand adverse conditions during transport. Other forms of resistance involve particle aggregation, either with members of the same taxon, which enhances the survival of those within the "aggregate" (Wadsworth et al., 2019), or with other particles such as cloud droplets or pollutants that act as vectors, enabling them to travel greater distances (Archer and Pointing, 2020). In this context, differences also arise depending on the nature of the particle acting as the vector. For example, combustion particulates may be less efficient vectors than mineral particles from desert dust and soil because they co-aerosolize with lower number of microorganisms and they are associated with toxic combustion products (Šantl-Temkiv et al., 2022).

Some airborne microorganisms keep metabolically active and can repair UV-induced DNA damage through mechanisms such as photoreactivation, potentially increasing their survival during atmospheric transport (Peccia & Hernandez, 2001). Others, however, can metabolize

carbon particles soluble in water droplets. Ervens and Amato (2020) described the activity of some bacteria metabolically active in the aqueous phase of clouds and on the surface or bulk phase of particles. They utilize small organic compounds leading to a decrease in Water-Soluble Organic Carbon mass within cloud droplets as bacteria convert these substrates into new organic products, biochemical energy, and CO₂ ("respiration"). In addition, these bacteria contribute to the net production of biological mass in the atmosphere, since that continuing with their growth and division cycles, they generate more mass that is called secondary biological aerosols. Microorganisms can also influence cloud microphysics, as some of them can act as cloud condensation nuclei or ice-nucleating particles, thereby potentially affecting cloud formation and precipitation (Bauer et al., 2003; Morris et al., 2004; Fröhlich-Nowoisky et al., 2016).

Taken together, these processes suggest that the atmosphere is not simply a medium for microbial transport, but a selective habitat in which environmental filtering may favor microorganisms with traits that enhance their persistence under atmospheric stress (Park & Fowler, 2026). Moreover, the physicochemical conditions experienced by airborne microorganisms may vary substantially among particles and atmospheric conditions, potentially influencing their survival and activity (Ervens et al., 2025). Microorganisms that remain viable in the atmosphere may therefore retain the potential to influence biogeochemical processes, including carbon cycling, while their role as ice-nucleating particles can influence the hydrological cycle (Šantl-Temkiv et al., 2022; Tang et al., 2022).

2.3 Deposition and colonization

As previously mentioned, microorganisms can influence various biogeochemical processes while being transported through the atmosphere. However, they also exert an influence upon deposition onto the surface. For instance, bioaerosols have been shown to constitute a flux of bioavailable phosphorus (P) in marine ecosystems, serving as a potential source of nutrients (Violaki et al., 2021). Therefore, and upon deposition, they alter the recipient ecosystem by changing its microbiological load as well as the levels of various chemical and molecular constituents. Furthermore, due to their pathogenic properties, they can also affect the health of organisms within that ecosystem, including humans, plants, animals, and other microorganisms.

There are two main deposition pathways: dry and wet deposition (Després et al., 2012). Dry deposition occurs in the absence of precipitation through processes such as gravitational settling, turbulent transport, impaction, and interception, whereas wet deposition occurs when airborne microorganisms are incorporated into cloud droplets or ice crystals through in-cloud scavenging and subsequently removed from the atmosphere by precipitation, including rain and snow. Wet deposition can also occur through below-cloud scavenging, in which falling precipitation captures airborne microorganisms as it passes through the atmosphere.

Fog can also facilitate the deposition of airborne microorganisms by providing liquid water droplets that may, for instance, be intercepted by vegetation and subsequently transferred to the underlying soil through processes such as throughfall and stemflow (Katata, 2014). Recent evidence has shown that fog can harbor viable microorganisms and thus represent an additional pathway for their transfer from the atmosphere to terrestrial ecosystems (Godoi et al., 2026). Furthermore, higher concentrations of cultivable bacterial and fungal bioaerosols have been observed on foggy days compared to non-foggy days, with a shift toward larger particle size

fractions; this suggests that fog can modify both the abundance and the physical characteristics of airborne microorganisms (Vishwakarma et al., 2024).

Atmospheric transport therefore does not end with microbial deposition. Rather, deposition marks the beginning of a second ecological filtering process that ultimately determines whether airborne microorganisms become transient visitors or persistent members of soil microbial communities. The different deposition pathways continuously replenish terrestrial ecosystems with microorganisms originating from both nearby and distant sources, thereby linking local communities to regional and global microbial metacommunities (Barberán et al., 2014; Šantl-Temkiv et al., 2022).

However, successful arrival is fundamentally different from successful establishment, with the location of landing being a deterministic factor (Tastassa et al., 2024). Similar to the ecological filters that shape plant and animal communities, deposited microorganisms must overcome a series of abiotic and biotic barriers before they can persist and contribute to ecosystem functioning. Abiotic filters include environmental compatibility, particularly soil moisture, temperature, nutrient availability, pH, and other physicochemical conditions that determine whether immigrants can survive after deposition. At the same time, resident microbial communities impose strong biotic filters through competition for resources, niche occupancy, antagonistic interactions, predation, and priority effects. Disturbance events, such as tillage, fire, flooding, or drought, may temporarily weaken these biotic barriers by creating vacant niches and reducing competitive exclusion, thereby increasing opportunities for colonization.

We propose the concept of airborne microbial immigration pressure as an atmospheric analogue to propagule pressure in invasion ecology. Whereas propagule pressure describes the number, frequency, and diversity of arriving organisms that influence invasion success, airborne microbial immigration pressure integrates the abundance, diversity, viability, and temporal continuity of microorganisms deposited from the atmosphere. Colonization success is expected to increase with repeated deposition events and greater taxonomic and functional diversity of immigrants, particularly when environmental conditions favor establishment or resident communities have been disturbed. Conversely, strong ecological filtering by intact resident microbiomes may prevent establishment despite continuous microbial deposition.

This framework shifts the perspective from microbial transport alone to microbial recruitment. Atmospheric deposition should therefore not be viewed merely as a passive redistribution of microorganisms but as a dynamic colonization process governed by the interaction between immigration pressure and ecological filtering. Quantifying these processes will be essential for predicting how atmospheric dispersal contributes to soil microbiome assembly, ecosystem resilience after disturbance, biological invasions, and the responses of terrestrial ecosystems to global environmental change.

3. Connectivity across spatial scales

3.1 Local connectivity

As discussed in the previous section, the deposition of microorganisms can modify the microbial load of the receiving ecosystem. Microorganisms can be transported over local, regional, and global scales, contributing to connectivity among ecosystems when they are deposited far from

their point of aerosolization (Kellogg and Griffin, 2006). At local and regional scales, transport may range from a few centimetres to several kilometres, depending on atmospheric conditions and the characteristics of the microorganisms involved. In most cases, soil airborne microorganisms are transported relatively short distances, resulting in frequent microbial exchange between the soil, circundant vegetation, and the atmosphere. For example, within forested environments, the canopy can act not only as a reservoir and filter of airborne microorganisms but also as a source from which microorganisms are subsequently re-aerosolized (Lympelopoulou, 2016; Winfrey et al., 2026). Such processes may facilitate microbial exchange between different compartments of the same ecosystem and between adjacent ecosystems.

At longer spatial scales, atmospheric transport can connect neighbouring agricultural fields, distinct ecosystems such as forests and grasslands, and natural, agricultural, and urban environments. As mentioned above, wind-driven transport, raindrop splash, and the resuspension of dust can all contribute to this connectivity. In particular, desert soils represent important sources and potential recipients of microorganisms (Schiro et al., 2022). During dust events, the aerosolization and atmospheric transport of mineral dust can therefore act as an efficient vector for the dispersal of microorganisms over hundreds to thousands of kilometres, linking geographically distant ecosystems (Navarro et al., 2024).

3.2 Long-distance connectivity ("teleconnections")

Atmospheric transport connects microbial communities across continents, oceans, and climatic zones, creating teleconnections that link ecosystems separated by thousands of kilometers. Unlike local dispersal, microorganisms entrained into the free troposphere can remain airborne for days to weeks before being deposited far from their source (Casamayor et al., 2023; Smith et al., 2012). Well-known examples include the transport of Saharan dust to Europe and the Americas, Asian dust plumes across the Pacific, transoceanic microbial dispersal, and wildfire smoke carrying microorganisms over continental scales. These events demonstrate that the atmosphere functions as a global dispersal network, continuously redistributing microorganisms across the Earth's surface.

Such long-distance dispersal has important implications for microbial biogeography. Atmospheric transport may connect otherwise isolated microbial metacommunities, facilitating gene flow, recolonization after disturbance, and the redistribution of functional traits across ecosystems (Reche et al., 2018). At the same time, these teleconnections can disseminate plant pathogens, human pathogens, antimicrobial resistance genes, and invasive microorganisms across political and biogeographic boundaries (Hadland et al., 2026; Polymenakou et al., 2008). The atmosphere therefore represents an often-overlooked mechanism linking local community assembly to global biodiversity patterns.

Future research should move beyond documenting long-distance dispersal events towards understanding their ecological significance. Key questions include how frequently atmospheric transport results in successful establishment, how teleconnections influence microbial evolution and ecosystem functioning, and how changing atmospheric circulation, dust storms, wildfires, and extreme weather events under global change will reshape patterns of microbial connectivity. Integrating atmospheric transport into metacommunity theory and Earth-system ecology offers a promising framework for predicting microbial biogeography in an increasingly connected biosphere.

4. Ecosystem consequences

4.1 Biodiversity

Atmospheric microbial dispersal continuously links soil communities at local and global scales, thereby increasing ecological connectivity across landscapes and continents. This bidirectional exchange (soil-to-atmosphere and atmosphere-to-soil) may maintain regional microbial diversity, and reduce the isolation of local communities by connecting microbial metacommunities. Furthermore, the atmosphere promotes recolonization following disturbance, acting as a reservoir of potential colonizers that can contribute to ecosystem resilience after disturbances such as droughts, fires, floods, or land-use changes (Malard and Pearce, 2022). At the same time, ecological filtering determines whether incoming microorganisms successfully establish themselves, implying that the deposition of aerosolized microorganisms does not necessarily translate into increased local diversity (Echenique-Subiabre et al., 2025). The interaction between immigration pressure and environmental filtering therefore represents a fundamental mechanism governing microbial community assembly across space and time.

4.2 Ecosystem functions and services

Whether atmospheric dispersal influences ecosystem functioning ultimately depends on the successful establishment and activity of deposited microorganisms (Reche et al., 2018). Airborne microbial exchange has the potential to alter decomposition, nutrient cycling, biological nitrogen fixation, methane cycling, carbon sequestration, and numerous other ecosystem processes by introducing new functional traits into resident communities. However, the functional consequences of microbial immigration remain poorly understood in microbial ecology (Walters et al., 2022). Most current studies quantify taxonomic changes following dispersal, whereas considerably less is known about whether newly arriving microorganisms contribute to ecosystem processes or simply remain transient members of the community. Resolving this distinction represents a major research frontier for understanding how atmospheric connectivity influences ecosystem functioning.

4.3 Plant microbiomes

The atmosphere provides a continuous source of microorganisms colonizing aboveground plant organs, including leaves, flowers, fruits, and stems (Xu et al., 2022), from where they may subsequently influence rhizosphere and root microbiome assembly. Atmospheric deposition therefore represents an important, yet often overlooked, pathway contributing to plant microbiome assembly alongside soil, seed, and insect vectors (Maignien et al., 2014). The composition of these airborne inocula may influence plant growth, nutrient acquisition, disease susceptibility, and tolerance to abiotic stress. In addition, pollen grains constitute another significant component of biological deposition, as they have species-specific microbiomes (Ambika Manirajan et al., 2016). Consequently, the deposition of pollen grains can simultaneously contribute to plant dispersal, the transport of microorganisms, and the input of organic matter into terrestrial ecosystems, as they can serve as a source of nutrition for the soil and other terrestrial organisms.

Considering the atmosphere as a microbial dispersal corridor therefore expands current concepts of plant microbiome assembly by explicitly incorporating regional and long-distance microbial connectivity.

4.4 Climate feedbacks

The relationship between atmospheric microbial dispersal and climate is fundamentally bidirectional. On the one hand, climatic conditions - including drought, strong winds, dust storms, wildfires, varying precipitation patterns, and atmospheric circulation - strongly regulate microbial aerosolization, atmospheric transport, and deposition (Tastassa et al., 2024). On the other hand, airborne microorganisms may actively influence atmospheric processes by acting as cloud condensation nuclei and ice-nucleating particles, thereby affecting cloud formation, precipitation, and potentially the climate itself (Fröhlich-Nowoisky et al., 2016; Burrows et al., 2022). Future climate change is expected to modify both sides of this feedback loop by altering the magnitude, frequency, and geographic extent of microbial transport while simultaneously changing the atmospheric conditions that determine microbial survival and dispersal (Casamayor et al., 2023). Understanding these reciprocal interactions is therefore essential for integrating microbial ecology into Earth-system science.

4.5 Ecosystem disservices

Atmospheric microbial connectivity is not universally beneficial. The same dispersal pathways that promote recolonization and ecosystem resilience may also facilitate the long-distance spread of harmful microorganisms and genes with important ecological, agricultural, and public-health consequences. Airborne dispersal contributes to the redistribution of plant and animal pathogens, potentially accelerating disease outbreaks in natural and agricultural ecosystems, while human pathogens transported through the atmosphere may influence exposure risks, particularly during dust storms, wildfires, and other extreme weather events (Kobziar et al., 2022; Kellog and Griffin, 2006). In addition, the atmosphere serves as a vector for pollen and microbially derived allergenic components, affecting air quality and respiratory health (Grewling et al., 2023; Jiménez-Urbe et al., 2026), and may facilitate the global dissemination of antibiotic resistance genes, raising concerns about their environmental spread, since antimicrobial resistance is projected to become an increasingly major global health burden by 2050 (GBD 2021 Antimicrobial Resistance Collaborators, 2024). Finally, toxin-producing microorganisms, including certain cyanobacteria and fungi, may be transported across large distances, introducing potentially harmful metabolites into new environments.

Climate change and increasing anthropogenic disturbance are likely to amplify many of these risks by increasing the frequency and intensity of wildfires, land degradation, and other processes capable of altering, relative to current conditions, the composition of aerosolized microbial communities and their patterns of long-distance transport. Atmospheric microbial connectivity should therefore be viewed as both an ecosystem service and an ecosystem disservice, depending on the identity, functional traits, and ecological roles of the organisms being dispersed. Recognizing this duality naturally links atmospheric microbial ecology with the One Health concept (see below), emphasizing that the health of soils, plants, animals, humans, and the atmosphere is intrinsically connected through the continuous movement of microorganisms across the biosphere.

5. One Health perspective

The continuous exchange of microorganisms between soils and the atmosphere provides a natural framework for extending the One Health concept to include atmospheric microbial connectivity (van Bruggen et al., 2019). Traditionally, One Health recognizes that the health of humans, animals, plants, and ecosystems is intrinsically interconnected (OHHLEP, 2022). More recently, the Food and Agriculture Organization of the United Nations (FAO, 2026) has highlighted

that microbiomes are present across diverse organisms and ecosystems, including the air. Because of that, we argue that the atmosphere should be viewed as an integral component of this framework because it continuously transports microorganisms, genes, and functional traits among these compartments, thereby linking ecological and public-health processes across local to global scales (Fröhlich-Nowoisky et al., 2016; Šantl-Temkiv et al., 2022).

Atmospheric microbial transport influences all components of the One Health continuum. Soil microorganisms colonize plant surfaces and contribute to plant microbiome assembly, affecting crop productivity, disease resistance, and resilience to environmental stress (Trivedi et al., 2020; Spooren et al., 2024). Conversely, atmospheric dispersal also facilitates the spread of plant pathogens, livestock pathogens, human pathogens, microbially allergenic derived components, toxin-producing microorganisms, and antibiotic resistance genes, thereby connecting ecosystem health with agricultural sustainability and human well-being. Air quality, microbial exposure in urban environments, and the atmospheric dissemination of antibiotic resistances further illustrate that microbial movement through the atmosphere has consequences extending far beyond ecosystem boundaries (Flies et al., 2020; Franchitti et al., 2022; Kormos et al., 2022).

Viewing soils and the atmosphere as a coupled microbiome therefore shifts One Health from a collection of connected compartments to a dynamic network linked by continuous microbial fluxes. This perspective suggests that sustainable land management, restoration, biosecurity, atmospheric pathogen surveillance, and biodiversity conservation should be considered as complementary strategies for maintaining healthy microbial exchange across the Earth system. Recognizing atmospheric microbial connectivity as a fundamental component of One Health opens new opportunities for integrating microbial ecology, atmospheric science, agriculture, epidemiology, and Earth-system research into a common predictive framework.

6. Implications for ecosystem management

Recognizing soils and the atmosphere as a coupled microbiome has important implications for ecosystem management. Land management not only modifies resident microbial communities but also influences the emission, transport, and deposition of microorganisms, thereby shaping microbial connectivity across landscapes. Sustainable management should therefore consider both local microbiome composition and the broader atmospheric processes that connect ecosystems (Eisenhauer et al., 2024).

In agricultural systems, practices such as reduced tillage, cover cropping, windbreaks, and soil moisture conservation may simultaneously reduce unnecessary aerosolization while maintaining beneficial microbial exchange (Gao, 2026). Restoration projects may benefit from considering atmospheric microbial recolonization as a complementary mechanism to local inoculation, particularly following large-scale disturbances. In urban environments, green infrastructure and dust management could promote healthier aerobiomes while reducing exposure to harmful microorganisms (Robinson et al., 2020; Matthews et al., 2024). Finally, integrating atmospheric surveillance with trajectory modelling may improve early warning systems for plant pathogens, invasive microorganisms, and antimicrobial resistance, strengthening biosecurity under a changing climate (Brodsky et al., 2023). Together, these examples illustrate that atmospheric microbial connectivity should become an integral component of ecosystem management, restoration planning, and environmental policy.

7. Future research frontiers

Despite rapid progress in atmospheric and soil microbiology, our understanding of air–soil microbiome connectivity remains in its infancy. We propose seven research frontiers that should guide the next generation of studies and establish a predictive framework for microbial connectivity across the Earth system and outline emerging opportunities in air–soil microbiome research (**Box 1**).

Frontier 1: Move from taxonomy to function

Most studies have focused on identifying which microorganisms are aerosolized, transported, and deposited. However, the ecological consequences of atmospheric dispersal depend primarily on the functional traits and capacities being transported rather than on taxonomic identities alone (Echenique-Subiabre et al., 2025). Future research should therefore integrate metagenomics, metatranscriptomics, metabolomics, and trait-based approaches to determine which metabolic pathways, ecological interactions, and ecosystem functions are redistributed through atmospheric transport. There are already a number of computational tools available today that enable the prediction of metagenomic functions from gene sequences, such as PICRUSt2 (Douglas et al., 2020), but these are primarily designed for human microbiomes. Further studies are needed in the fields of ecology and environmental sampling, because of that, moving from descriptive inventories towards functional ecology will be essential for understanding how microbial dispersal influences ecosystem functioning.

Frontier 2: Quantify global microbial fluxes

Although billions of microorganisms are exchanged between soils and the atmosphere every day, their global magnitude remains almost completely unknown. Similar to carbon or nitrogen budgets, microbial ecology now requires analyzing microbial flux budgets that quantify the movement of microbial cells, biomass, as well as genes and functional traits among ecosystems (Louca, 2022; Choudoir and deAngelis, 2022). Such budgets would enable direct comparisons among ecosystems and provide the quantitative foundation for incorporating microbial dispersal into Earth-system models. To this end, it is also important to understand which types of terrestrial sources contribute microorganisms to the atmosphere, as different microbial groups may differ in their aerosolisation efficiency. For example, the aerosolisation of bacteria may not occur to the same extent as that of fungi (He et al., 2019), potentially affecting the overall number and composition of microorganisms emitted into the atmosphere.

Frontier 3: Determine colonization success

Transport does not necessarily result in establishment (Custer et al., 2022). Future research must therefore distinguish among the sequential processes of arrival, survival, establishment, growth, and functional integration of deposited microorganisms. Quantifying microbial immigration pressure together with ecological filtering will allow predictions of when atmospheric dispersal merely redistributes microorganisms and when it fundamentally alters resident microbiomes and ecosystem functioning.

Frontier 4: Integrate atmospheric science and microbial ecology

Atmospheric and microbial sciences have usually developed independently despite studying two tightly connected components of the same Earth system. Bridging these disciplines more

consistently will require combining atmospheric transport models, meteorological observations, remote sensing, microbial ecology, and Earth-system modelling into unified predictive frameworks. Such interdisciplinary approaches will substantially improve predictions of microbial dispersal pathways and their ecological consequences under future environmental change.

Frontier 5: Evolution during atmospheric transport

The atmosphere is commonly viewed as a transport corridor, yet it may also act as an evolutionary filter (Amato et al., 2023). Strong selection imposed by ultraviolet radiation, desiccation, oxidative stress, temperature fluctuations, and nutrient limitation may favor specific microbial traits (Park and Fowler, 2026), while prolonged transport may influence mutation rates, dormancy, and horizontal gene transfer. Understanding whether atmospheric transport simply redistributes microbial diversity or actively shapes microbial evolution represents an exciting frontier in aerobiology.

Frontier 6: Predictive Earth–microbiome connectivity

The field should move towards predicting the origin, transport, establishment, and ecological consequences of microbial dispersal across the globe. Achieving this goal will require integrating microbial traits, atmospheric circulation, environmental filtering, ecological interactions, and climate projections into coupled Earth-system models. Such predictive frameworks could forecast microbial connectivity under future climates, identify emerging biosecurity risks, improve restoration planning, and reveal how atmospheric microbial exchange contributes to the resilience of terrestrial ecosystems. More broadly, recognizing the atmosphere as the circulatory system of the terrestrial microbiome has the potential to transform our understanding of microbial biogeography and establish atmospheric connectivity as a fundamental process governing biodiversity and ecosystem functioning under global environmental change.

Frontier 7: Earth-microbiome connectivity and extreme events

Ultimately, when studying the Earth-microbiome connectivity, it is also important to consider how climate change and increasing environmental disturbances will reshape atmospheric microbial connectivity. Prolonged droughts have such significant consequences for vegetation and soil that the resulting changes can influence the aerosolisation of microorganisms and, consequently, which microbiome is transported and ultimately deposited in the recipient ecosystem (Qi et al., 2023). Similarly, wildfires represent a major source of particulate emissions, including the microorganisms. Owing to the nature of these emissions, they are capable of reaching high layers of the atmosphere and travelling long distances, thereby connecting geographically distant ecosystems (Kozbiar et al., 2022). Analysing connectivity between terrestrial and atmospheric microbiomes during and immediately after extreme events such as those described above will help us better understand how disturbances reshape microbial communities and how these changes may influence recipient ecosystems and their functioning.

Box 1: Emerging opportunities in air–soil microbiome research

Earth microbiome

Viewing the atmosphere as the circulatory system of the terrestrial microbiome provides a unifying framework that links soils, vegetation, oceans, and the atmosphere into one interconnected Earth microbiome.

Wildfire microbiomes

Wildfires likely redistribute unique microbial communities over continental scales, yet their ecological consequences remain almost completely unexplored.

Resistome transport

Atmospheric transport may become an important pathway for the global dissemination of antimicrobial resistance genes, linking ecosystem processes with public health.

Airborne viromes

Viruses, including bacteriophages and plant viruses, are probably transported alongside bacteria and fungi, but their ecological roles remain almost unknown.

Microbial dark matter

Most airborne microorganisms remain uncultured and functionally uncharacterized, suggesting that atmospheric transport redistributes an enormous hidden component of Earth's biodiversity.

Trait-based aerobiology

Future studies should go beyond purely taxonomic assessment and identify the traits determining aerosolization, atmospheric persistence, deposition, colonization, and ecosystem impacts.

Machine learning

Combining atmospheric trajectory models with machine learning may allow forecasts of microbial dispersal, pathogen outbreaks, and ecosystem connectivity under future climates.

8. References

- Acosta-Martínez, V., Van Pelt, S., Moore-Kucera, J., Baddock, M. C., and Zobeck, T. M. (2015). Microbiology of wind-eroded sediments: Current knowledge and future research directions. *Aeolian Research*, 18, 99–113. <https://doi.org/10.1016/j.aeolia.2015.06.001>
- Amato P, Mathonat F, Nuñez Lopez L, Péguilhan R, Bourhane Z, Rossi F, Vyskocil J, Joly M and Ervens B (2023) The aeromicrobiome: the selective and dynamic outer-layer of the Earth's microbiome. *Front. Microbiol.* 14:1186847. doi: 10.3389/fmicb.2023.1186847
- Manirajan, B. A., Ratering, S., Rusch, V., Schwiertz, A., Geissler-Plaum, R., Cardinale, M., and Schnell, S. (2016). Bacterial microbiota associated with flower pollen is influenced by pollination type and shows a high degree of diversity and species-specificity. *Environmental Microbiology*, 18(12), 5161–5174. <https://doi.org/10.1111/1462-2920.13524>
- Archer, S.D.J., Pointing, S.B. (2020). Anthropogenic impact on the atmospheric microbiome. *Nat Microbiol* 5, 229–231. <https://doi.org/10.1038/s41564-019-0650-z>

- 554 - Bauer, H., Giebl, H., Hitzenberger, R., Kasper-Giebl, A., Reischl, G., Zibuschka, F., and
555 Puxbaum, H. (2003). Airborne bacteria as cloud condensation nuclei. *Journal of*
556 *Geophysical Research: Atmospheres*, 108(D21), 4658.
557 <https://doi.org/10.1029/2003JD003545>
- 558 - Barberán, A., Ladau, J., Leff, J. W., Pollard, K. S., Menninger, H. L., Dunn, R. R., & Fierer,
559 N. (2015). Continental-scale distributions of dust-associated bacteria and fungi.
560 *Proceedings of the National Academy of Sciences*, 112(18), 5756–5761.
561 <https://doi.org/10.1073/pnas.1420815112>
- 562 - Bourouiba, L. (2021). The fluid dynamics of disease transmission. *Annual Review of Fluid*
563 *Mechanics*, 53, 473–508. <https://doi.org/10.1146/annurev-fluid-060220-113712>
- 564 - Brodsky, H. K., Calderón, R., Hamilton, D. S., Li, L., Miles, A., Pavlick, R., Gold, K. M.,
565 Crandall, S. G., and Mahowald, N. (2023). Assessing long-distance atmospheric transport
566 of soilborne plant pathogens. *Environmental Research Letters*, 18(10), 104021.
567 <https://doi.org/10.1088/1748-9326/acf50c>
- 568 - Burrows, S. M., McCluskey, C. S., Cornwell, G., Steinke, I., Zhang, K., Zhao, B., et al.
569 (2022). Ice-nucleating particles that impact clouds and climate: Observational and
570 modeling research needs. *Reviews of Geophysics*, 60, e2021RG000745.
571 <https://doi.org/10.1029/2021RG000745>
- 572 - Casamayor, E. O., Cáliz, J., Triadó-Margarit, X., and Pointing, S. B. (2023). Understanding
573 atmospheric intercontinental dispersal of harmful microorganisms. *Current Opinion in*
574 *Biotechnology*, 81, 102945. <https://doi.org/10.1016/j.copbio.2023.102945>
- 575 - Choudoir, M.J. and DeAngelis, K.M. (2022). A framework for integrating microbial
576 dispersal modes into soil ecosystem ecology. *iScience* 10;25(3):103887. doi:
577 10.1016/j.isci.2022.103887
- 578 - Custer, G.F., Bresciani, L. and Dini-Andreote, F. (2022) Ecological and Evolutionary
579 Implications of Microbial Dispersal. *Front. Microbiol.* 13:855859. doi:
580 10.3389/fmicb.2022.855859
- 581 - Deutscher Wetterdienst. (n.d.). *Particle size-distribution*.
582 https://www.dwd.de/EN/research/observing_atmosphere/composition_atmosphere/aerosol/cont_nav/particle_size_distribution_node.html
583
- 584 - Després, V. R., Huffman, J. A., Burrows, S. M., Hoose, C., Safatov, A. S., Buryak, G.,
585 Fröhlich-Nowoisky, J., Elbert, W., Andreae, M. O., Pöschl, U., and Jaenicke, R. (2012).
586 Primary biological aerosol particles in the atmosphere: A review. *Tellus B: Chemical and*
587 *Physical Meteorology*, 64(1), 15598. <https://doi.org/10.3402/tellusb.v64i0.15598>
- 588 - Douglas, G. M., Maffei, V. J., Zaneveld, J. R., Yurgel, S. N., Brown, J. R., Taylor, C. M.,
589 Huttenhower, C., Langille, M. G. I., and Morgan, X. C. (2020). PICRUSt2 for prediction of
590 metagenome functions from marker gene sequences. *Nature Biotechnology*, 38(6), 685–
591 688. doi.org
- 592 - Echenique-Subiabre, I., Jackrel, S.L., McCarren, J., James, C.C., Perez-Coronel, E., Tran,
593 C., Perreault, M., Farah, U., White, P.S., Baker, H.K., Wall, C.B., Sager, L., Becker, S.,

594 Barton, A.D., and Shurin, J.B. (2025). Traits determine dispersal and colonization abilities
595 of microbes. *Appl Environ Microbiol* 91: e02055-24. <https://doi.org/10.1128/aem.02055-24>

596 - Eisenhauer, N., Frank, K., Weigelt, A., Bartkowski, B., Beugnon, R., Liebal, K., et al.
597 (2024). A belowground perspective on the nexus between biodiversity change, climate
598 change, and human well-being. *J Sustain Agric Environ.* 3: e212108.
599 <https://doi.org/10.1002/sae2.12108>

600 - Emeis, S. (2013). *Wind Energy Meteorology: Atmospheric Physics for Wind Power*
601 *Generation*. Springer, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-642-30523-8>

602 - Ervens, B. and Amato, P. (2020). The global impact of bacterial processes on carbon
603 mass, *Atmos. Chem. Phys.*, 20, 1777–1794, <https://doi.org/10.5194/acp-20-1777-2020>

604 - Ervens, B., Amato, P., Aregahegn, K., Joly, M., Khaled, A., Labed-Veydert, T., Mathonat,
605 F., Nuñez López, L., Péguilhan, R., and Zhang, M. (2025). Ideas and perspectives:
606 Microorganisms in the air through the lenses of atmospheric chemistry and microphysics.
607 *Biogeosciences*, 22(1), 243–256. <https://doi.org/10.5194/bg-22-243-2025>

608 - Flies, E. J., Clarke, L.J., Brook, BW., and Jones, P. (2020). Urbanisation reduces the
609 abundance and diversity of airborne microbes—but what does that mean for our health?
610 A systematic review. *Science of the Total Environment*, 738, 140337.
611 <https://doi.org/10.1016/j.scitotenv.2020.140337>

612 - Food and Agriculture Organization of the United Nations (FAO). (2026). *Integrating*
613 *microbial systems into the One Health approach*. [https://www.fao.org/one-](https://www.fao.org/one-health/highlights/highlights-detail/integrating-microbial-systems-into-the-one-health-approach/en)
614 [health/highlights/highlights-detail/integrating-microbial-systems-into-the-one-health-](https://www.fao.org/one-health/highlights/highlights-detail/integrating-microbial-systems-into-the-one-health-approach/en)
615 [approach/en](https://www.fao.org/one-health/highlights/highlights-detail/integrating-microbial-systems-into-the-one-health-approach/en)

616 - Franchitti, E., Caredda, C., Anedda, E., and Traversi, D. (2022). Urban Aerobiome and
617 Effects on Human Health: A Systematic Review and Missing Evidence. *Atmosphere*, 13,
618 1148. <https://doi.org/10.3390/atmos13071148>

619 - Fröhlich-Nowoisky, J., Kampf, C. J., Weber, B., Huffman, J. A., Pöhlker, C., Andreae, M.
620 O., Lang-Yona, N., Burrows, S. M., Gunthe, S. S., Elbert, W., Su, H., Hoor, P., Thines, E.,
621 Hoffmann, T., Després, V. R., and Pöschl, U. (2016). Bioaerosols in the Earth system:
622 Climate, health, and ecosystem interactions. *Atmospheric Research*, 182, 346–376.
623 <https://doi.org/10.1016/j.atmosres.2016.07.018>

624 - Gao, P. (2026). Healthy soil as the invisible determinant of a healthy environment: A critical
625 review. *Soil & Environmental Health*, 4(2), 100214.
626 <https://doi.org/10.1016/j.seh.2026.100214>

627 - GBD 2021 Antimicrobial Resistance Collaborators. (2024). Global burden of bacterial
628 antimicrobial resistance 1990–2021: A systematic analysis with forecasts to 2050. *The*
629 *Lancet*, 404(10459), 1199–1226. [https://doi.org/10.1016/S0140-6736\(24\)01867-1](https://doi.org/10.1016/S0140-6736(24)01867-1)

630 - Godoi, R. H. M., Hara, E. L. Y., Sebben, B. G., Taylor, P. E., Castro e Silva, D. M., Brill,
631 S., Duo Filho, V. B., Valdameri, G., Huergo, L. F., Ferreira, R. R., Dias-Junior, C. Q.,
632 Mantoani, M. C., Gonçalves, F. L. T., Albrecht, R. I., Lata, N. N., Vandergrift, G., China,
633 S., Yamamoto, C. I., Marques, R. F. C., ... Andreae, M. O. (2026). *Amazonian fog harbors*
634 *viable microbes*. *Communications Earth & Environment*, 7, 223.
635 <https://doi.org/10.1038/s43247-026-03233-4>

- 636 - Grewling, Ł., Ribeiro, H., Antunes, C., Apangu, G. P., Çelenk, S., Costa, A., Eguiluz-
637 Gracia, I., Galveias, A., Gonzalez Roldan, N., Lika, M., Magyar, D., Martinez-Bracero, M.,
638 Ørby, P., O'Connor, D., Marchã Penha, A., Pereira, S., Pérez-Badia, R., Rodinkova, V.,
639 Xhetani, M., Šauliene, I., and Skjøth, C. A. (2023). Outdoor airborne allergens:
640 Characterization, behavior and monitoring in Europe. *Science of the Total Environment*,
641 905, 167042. <https://doi.org/10.1016/j.scitotenv.2023.167042>
- 642 - Griffin, D.W. (2021). The concept of evanescent microbial ecosystems in Earth's
643 atmosphere. In *Microbial Ecology of Extreme Environments* (pp. 65–77). Springer.
644 https://doi.org/10.1007/978-3-030-63512-1_5
- 645 - Gusareva, E. S., Acerbi, E., Lau, K. J. X., Luhung, I., Premkrishnan, B. N. V., Kolundžija,
646 S., Purbojati, R. W., Wong, A., Houghton, J. N. I., Miller, D., Gaultier, N. E., Heinle, C. E.,
647 Clare, M. E., Vettath, V. K., Kee, C., Lim, S. B. Y., Chénard, C., Phung, W. J., Kushwaha,
648 K. K., ... Schuster, S. C. (2019). Microbial communities in the tropical air ecosystem follow
649 a precise diel cycle. *Proceedings of the National Academy of Sciences*, 116(24), 11624–
650 11633. <https://doi.org/10.1073/pnas.1900166116>
- 651 - Hadland N, Hamilton CW, Schroedl P, Calabrese F, Marlow J, and Duhamel S. (2026).
652 Microbial dispersal from a hyperactive sandsheet in the Icelandic Highland. *Sci Total*
653 *Environ.* 15;1025:181659. doi: 10.1016/j.scitotenv.2026.181659
- 654 - He, P., Wei, S., Shao, L., and Lü, F. (2019). Aerosolization behavior of prokaryotes and
655 fungi during composting of vegetable waste. *Waste Manag.* 15; 89:103-113. doi:
656 10.1016/j.wasman.2019.04.008
- 657 - Jiménez-Urbe, D. A., Acevedo-Barrios, R., Rubiano-Labrador, C., and Cariñanos, P.
658 (2026). Relationship of airborne fungal spores to epidemiological data on respiratory
659 disease: A systematic review. *Aerobiologia*, 42, 11. [https://doi.org/10.1007/s10453-025-](https://doi.org/10.1007/s10453-025-09890-w)
660 [09890-w](https://doi.org/10.1007/s10453-025-09890-w)
- 661 - Joung, Y., Ge, Z. and Buie, C. (2017). Bioaerosol generation by raindrops on soil. *Nat*
662 *Commun* 8, 14668. <https://doi.org/10.1038/ncomms14668>
- 663 - Katata, G. (2014). Fogwater deposition modeling for terrestrial ecosystems: A review of
664 developments and measurements. *Journal of Geophysical Research: Atmospheres*, 119,
665 8137–8159. <https://doi.org/10.1002/2014JD021669>
- 666 - Kellogg, C. A., and Griffin, D. W. (2006). Aerobiology and the global transport of desert
667 dust. *Trends in Ecology & Evolution*, 21(11), 638–644.
668 <https://doi.org/10.1016/j.tree.2006.07.004>
- 669 - Kobziar, L. N., Vuono, D., Moore, R., Christner, B. C., Dean, T., Betancourt, D., Watts, A.
670 C., Aurell, J., and Gullett, B. (2022). Wildland fire smoke alters the composition, diversity,
671 and potential atmospheric function of microbial life in the aerobiome. *ISME*
672 *Communications*, 2(1), 8. <https://doi.org/10.1038/s43705-022-00089-5>
- 673 - Kormos, D., Lin, K., Pruden, A., and Marr, L. C. (2022). Critical review of antibiotic
674 resistance genes in the atmosphere. *Environmental Science: Processes & Impacts*, 24(6),
675 870–883. <https://doi.org/10.1039/D2EM00091A>

- 676 - Lighthart, B. (1984). Microbial aerosols: Estimated contribution of combine harvesting to
677 an airshed. *Applied and Environmental Microbiology*, 47(2), 430–432.
678 <https://doi.org/10.1128/AEM.47.2.430-432.1984>
- 679 - Lympelopoulou, D.S, Adams, R.I, and Lindow, S.E. (2016). Contribution of Vegetation to
680 the Microbial Composition of Nearby Outdoor Air. *Appl Environ Microbiol.* 13;82(13):3822-
681 33. doi: 10.1128/AEM.00610-16
- 682 - Louca, S. (2022). The rates of global bacterial and archaeal dispersal. *ISME J* 16, 159–
683 167. <https://doi.org/10.1038/s41396-021-01069-8>
- 684 - Maignien, L., DeForce, E.A., Chafee, M.E., Eren, A.M. and Simmons, S.L. (2014).
685 Ecological succession and stochastic variation in the assembly of *Arabidopsis thaliana*
686 phyllosphere communities. *mBio.* 21;5(1): e00682-13. doi: 10.1128/mBio.00682-13.
- 687 - Malard LA, and Pearce DA. (2022). Bacterial Colonisation: From Airborne Dispersal to
688 Integration Within the Soil Community. *Front Microbiol.* 9; 13:782789. doi:
689 10.3389/fmicb.2022.782789
- 690 - Mayol, E., Jiménez, M.A., Herndl, G.J., Duarte, C.M. and Arrieta, J.M. (2014). Resolving
691 the abundance and air-sea fluxes of airborne microorganisms in the North Atlantic Ocean.
692 *Front Microbiol.* 31; 5:557. doi: 10.3389/fmicb.2014.00557. Erratum in: *Front Microbiol.*
693 2017 Oct 13; 8:1971. doi: 10.3389/fmicb.2017.01971.
- 694 - Matthews, K., Cavagnaro, T., Weinstein, P., and Stanhope, J. (2024). Health by design;
695 Optimising our urban environmental microbiomes for human health. *Environmental*
696 *Research*, 257, 119226. <https://doi.org/10.1016/j.envres.2024.119226>
- 697 - Morales-Baquero, R., and C. Pérez-Martínez (2016). Saharan versus local influence on
698 atmospheric aerosol deposition in the southern Iberian Peninsula: Significance for N and
699 P inputs, *Global Biogeochem. Cycles*, 30, 501–513, doi:10.1002/2015GB005254.
- 700 - Morris, C. E., Georgakopoulos, D. G., and Sands, D. C. (2004). Ice nucleation active
701 bacteria and their potential role in precipitation. *Journal de Physique IV*, 121, 87–103.
702 <https://doi.org/10.1051/jp4:2004121004>
- 703 - Navarro, A., del Moral, A., Weber, B., Weber, J., Molinero, A., Delgado, R., Párraga, J.,
704 and Martínez-Checa, F. (2024). Microbial composition of Saharan dust plumes deposited
705 as red rain in Granada (Southern Spain). *Science of the Total Environment*, 913, 169745.
706 <https://doi.org/10.1016/j.scitotenv.2023.169745>
- 707 - One Health High-Level Expert Panel (OHHLEP), Adisasmito, W. B., Almuhairi, S.,
708 Behravesh, C. B., Bilivogui, P., Bukachi, S. A., et al. (2022). One Health: A new definition
709 for a sustainable and healthy future. *PLOS Pathogens*, 18(6), e1010537.
710 <https://doi.org/10.1371/journal.ppat.1010537>
- 711 - Park, J., and Fowler, S. J. (2026). Airborne Bacterial Communities: Diversity, Survival
712 Strategies and Functional Roles in the Atmosphere. *Environmental Microbiology Reports*
713 18, no. 1: e70274. <https://doi.org/10.1111/1758-2229.70274>.
- 714 - Peccia, J. and Hernandez, M. (2001). Photoreactivation in Airborne *Mycobacterium*
715 *parafortuitum*. *Appl Environ Microbiol* 67, [https://doi.org/10.1128/AEM.67.9.4225-](https://doi.org/10.1128/AEM.67.9.4225-4232.2001)
716 4232.2001

- 717 - Poirier, S., Rondeau-Leclaire, J., Faticov, M., Roy, A., Lajeunesse, G., Lucier, J.F., Tardif,
718 S., Kembel, S.W., Ziter, C., Laprise, C., Paquette, A., Girard, C., and Laforest-Lapointe, I.
719 (2026). Season and city shape urban bioaerosol composition beyond vegetation and
720 socioeconomic gradients. *Sci Total Environ.* 1;1023:181623. doi:
721 10.1016/j.scitotenv.2026.181623.
- 722 - Polymenakou, P. N., Mandalakis, M., Stephanou, E. G., and Tselepidis, A. (2008).
723 Particle size distribution of airborne microorganisms and pathogens during an intense
724 African dust event in the eastern Mediterranean. *Environmental Health Perspectives*,
725 116(3), 292–296. <https://doi.org/10.1289/ehp.10684>
- 726 - Qi, J., Huang, Z., Xue, F., Gao, Z., Maki, T., Zhang, Z., Liu, K., Ji, M., and Liu, Y. (2023).
727 Aridification alters the diversity of airborne bacteria in drylands of China. *Atmospheric*
728 *Environment*, 315, 120135. <https://doi.org/10.1016/j.atmosenv.2023.120135>
- 729 - Reche, I., D'Orta, G., Mladenov, N., Winget, D. M., and Suttle, C. A. (2018). Deposition
730 rates of viruses and bacteria above the atmospheric boundary layer. *The ISME Journal*,
731 12, 1154–1162. <https://doi.org/10.1038/s41396-017-0042-4>
- 732 - Robinson, J. M., Cando-Dumancela, C., Liddicoat, C., Weinstein, P., Cameron, R., and
733 Breed, M. F. (2020). Vertical stratification in urban green space aerobiomes.
734 *Environmental Health Perspectives*, 128(11), 117008. <https://doi.org/10.1289/EHP7807>
- 735 - Sánchez-Parra, B., Núñez, A., García, A. M., Campoy, P., and Moreno, D. A. (2021).
736 Distribution of airborne pollen, fungi and bacteria at four altitudes using high-throughput
737 DNA sequencing. *Atmospheric Research*, 249, 105306.
738 <https://doi.org/10.1016/j.atmosres.2020.105306>
- 739 - Šantl-Temkiv, T., Amato, P., Casamayor, E. O., Lee, P. K. H., and Pointing, S. B. (2022).
740 Microbial ecology of the atmosphere. *FEMS Microbiology Reviews*, 46(4), fuac009.
741 <https://doi.org/10.1093/femsre/fuac009>
- 742 - Schiro, G., Chen, Y., Blankinship, J.C. and Barberán, A. (2022). Ride the dust: linking dust
743 dispersal and spatial distribution of microorganisms across an arid landscape. *Environ*
744 *Microbiol*, 24: 4094-4107. <https://doi.org/10.1111/1462-2920.15998>
- 745 - Smith, D. J., Jaffe, D. A., Birmele, M. N., Griffin, D. W., Schuerger, A. C., Hee, J., and
746 Roberts, M. S. (2012). Free tropospheric transport of microorganisms from Asia to North
747 America. *Microbial Ecology*, 64, 973–985. <https://doi.org/10.1007/s00248-012-0088-9>
- 748 - Sokol, N. W., Slessarev, E., Marschmann, G. L., Nicolas, A., Blazewicz, S. J., Brodie, E.
749 L., Firestone, M. K., Foley, M. M., Hestrin, R., Hungate, B. A., Koch, B. J., Stone, B. W.,
750 Sullivan, M. B., Zablocki, O., LLNL Soil Microbiome Consortium, & Pett-Ridge, J. (2022).
751 Life and death in the soil microbiome: how ecological processes influence
752 biogeochemistry. *Nat Rev Microbiol* 20, 415–430. [https://doi.org/10.1038/s41579-022-](https://doi.org/10.1038/s41579-022-00695-z)
753 00695-z
- 754 - Spooren, J., van Bentum, S., Thomashow, L. S., Pieterse, C. M. J., Weller, D. M., and
755 Berendsen, R. L. (2024). Plant-driven assembly of disease-suppressive soil microbiomes.
756 *Annual Review of Phytopathology*, 62, 1–30. [https://doi.org/10.1146/annurev-phyto-](https://doi.org/10.1146/annurev-phyto-021622-100127)
757 021622-100127

- 758 - Stull, R.B. (1988). Mean Boundary Layer Characteristics. In: Stull, R.B. (eds) An
759 Introduction to Boundary Layer Meteorology. Atmospheric Sciences Library, vol 13.
760 Springer, Dordrecht. https://doi.org/10.1007/978-94-009-3027-8_1
- 761 - Tang, K., Sánchez-Parra, B., Yordanova, P., Wehking, J., Backes, A. T., Pickersgill, D. A.,
762 Maier, S., Sciare, J., Pöschl, U., Weber, B., and Fröhlich-Nowoisky, J. (2022). Bioaerosols
763 and atmospheric ice nuclei in a Mediterranean dryland: community changes related to
764 rainfall, *Biogeosciences*, 19, 71–91, <https://doi.org/10.5194/bg-19-71-2022>
- 765 - Tastassa, A. C., Sharaby, Y., and Lang-Yona, N. (2024). Aeromicrobiology: A global
766 review of the cycling and relationships of bioaerosols with the atmosphere. *Science of the*
767 *Total Environment*, 912, 168478. <https://doi.org/10.1016/j.scitotenv.2023.168478>
- 768 - Tesson, S. V. M., Skjøth, C. A., and Šantl-Temkiv, T. (2016). Airborne microalgae:
769 Insights, opportunities, and challenges. *Applied and Environmental Microbiology*, 82(7),
770 1978–1991. <https://doi.org/10.1128/AEM.03333-15>
- 771 - Trail, F. (2007). Fungal cannons: explosive spore discharge in the Ascomycota. *FEMS*
772 *Microbiol. Lett.* 276 (1), 12–18. <https://doi.org/10.1111/j.1574-6968.2007.00900.x>
773 (accessed 2022/06/21/).
- 774 - Trivedi, P., Leach, J.E., Tringe, S.G., Sa,T. and Singh, B.K. (2020). Plant–microbiome
775 interactions: from community assembly to plant health. *Nat Rev Microbiol* 18, 607–62.
776 <https://doi.org/10.1038/s41579-020-0412-1>
- 777 - van Bruggen, A. H. C., Goss, E. M., Havelaar, A., van Diepeningen, A. D., Finckh, M. R.,
778 and Morris, J. G. (2019). One Health—Cycling of diverse microbial communities as a
779 connecting force for soil, plant, animal, human and ecosystem health. *Science of the Total*
780 *Environment*, 664, 927–937. <https://doi.org/10.1016/j.scitotenv.2019.02.091>
- 781 - Violaki, K., Nenes, A., Tsagkaraki, M., Paglione, M., Jacquet, S., Sempéré, R., and
782 Panagiotopoulos, C. (2021). Bioaerosols and dust are the dominant sources of organic P
783 in atmospheric particles. *Climate and Atmospheric Science* 4:63;
784 <https://doi.org/10.1038/s41612-021-00215-5>
- 785 - Vishwakarma, Y. K., Ram, K., Gogoi, M. M., Banerjee, T., and Singh, R. S. (2024). Size-
786 segregated characteristics of bioaerosols during foggy and non-foggy days of winter,
787 meteorological implications, and health risk assessment. *Environmental Science:*
788 *Advances*, 3(8), 1163–1172. <https://doi.org/10.1039/D4VA00108G>
- 789 - Wadsworth J, Rettberg P, Cockell CS. Aggregated Cell Masses Provide Protection against
790 Space Extremes and a Microhabitat for Hitchhiking Co-Inhabitants (2019). *Astrobiology*
791 19 (8): 995-1007. doi:10.1089/ast.2018.1924
- 792 - Walters, K. E., Capocchi, J. K., Albright, M. B. N., Hao, Z., Brodie, E. L., and Martiny, J.
793 B. H. (2022). Routes and rates of bacterial dispersal impact surface soil microbiome
794 composition and functioning. *The ISME Journal*, 16, 2295–2304.
795 <https://doi.org/10.1038/s41396-022-01269-w>

- 796 - Winfrey, C.C., Socualaya-Torres, A.A., Resasco, J., Fierer, N. (2026). Sources and traits
797 of bacteria and fungi found in the near-surface atmosphere. *Appl Environ Microbiol*
798 92:e02348-25. <https://doi.org/10.1128/aem.02348-25>
- 799 - Xu, N., Zhao, Q., Zhang, Z., Zhang, Q., Wang, Y., Qin, G., Ke, M., Qiu, D., Peijnenburg,
800 W. J. G. M., Lu, T., and Qian, H. (2022). Phyllosphere microorganisms: Sources, drivers,
801 and their interactions with plant hosts. *Journal of Agricultural and Food Chemistry*, 70(16),
802 4860–4870. <https://doi.org/10.1021/acs.jafc.2c01113>
803