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Review

Potential planetary health impacts of the airborne plastisphere

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SUMMARY

Microplastics are a ubiquitous yet long-overlooked component of airborne particulate matter. The surface of these plastic particles provides a unique niche for microorganisms, collectively known as the plastisphere. The plastisphere in aquatic and terrestrial ecosystems harbors microbial communities with distinct compositions, structures, and functional profiles, posing potential planetary health risks. The characteristics, fate, and impacts of the microbiome associated with airborne microplastics, however, remain largely unknown. In this review, we fill the knowledge gaps by exploring how airborne microplastics serve as key habitats for microorganisms and the potential planetary health implications. We show that microplastics are expected to carry and sustain microorganisms over long distances and timescales in air, potentially dispersing pathogens, antibiotic-resistance genes, and other bioactive agents across ecosystems. These interactions may perturb ecological processes and biological health on a planetary scale. Interdisciplinary research and innovative methodologies are urgently required to better understand and mitigate the airborne plastisphere risks.

INTRODUCTION

Plastic pollution is one of the most pressing environmental issues of the Anthropocene, posing critical challenges for sustainability of the Earth system.[1–4] It has been proposed that humans have surpassed the planetary boundaries of several environmental pollutants, including plastics.[5–7] These pollutants have pervaded the entire Earth system,[4,8–11] exerting direct and indirect and short- and long-term effects on humans and other organisms,[12–17] while exacerbating the impacts of all planetary boundaries.[5,18,19]

Microplastics (plastic particles <5 mm) are recognized as a ubiquitous component of airborne particulate matter (PM).[20–25] For example, recent estimates report that >13% of airborne $PM_{2.5}$ (PM $\leq$ 2.5 μm) in Shanghai is composed of microplastics.[26] The abundance of microplastic particles in air can reach tens of thousands of particles per cubic meter in some urban areas[27] (Figure 1). Recent estimates show that adults can be exposed to over 10,000 microplastic particles via air each year,[28] potentially posing significant human health risks.[14] Even in protected areas and above remote oceans, airborne microplastics are commonly detected (Figure 1). For example, the average microplastic deposition rates from the coastal city of Auckland in 2020 were between 92 and 151 kg km^{-2} per year.[29] Approximately 2–7 kg km^{-2} and >1,000 metric tons/year of microplastics were transported via the atmosphere and deposited in remote wilderness areas in the western United States during 2017–2019.[20] Between 0.013 and 25 million metric tons/year of microplastics were estimated to be transported in the atmosphere and deposited into the ocean via air-sea exchange.[30]

The impacts of plastics on organisms and the environment are not limited to the particles themselves, but also include impacts induced by their associated chemicals and microorganisms.[31–35] Microorganisms associated with plastics are a novel concern that has recently garnered a significant increase in attention by scientists and policymakers.[33,35–39] Plastics provide a specific habitat for microorganisms, resulting in a microecosystem where plastic is the substrate, referred to as "the plastisphere."[33,35,36] In aquatic or terrestrial ecosystems, the plastisphere fosters unique microbial community structures and functions, with demonstrated higher abundances of pathogens, antibiotic-resistant bacteria, and viruses compared to the surrounding environment, posing potential planetary health risks.[35,37–45] However, the properties of the plastisphere in air and its potential impacts are largely unknown.[46]

The atmosphere may be the largest microbial ecosystem on Earth, containing an estimated 10^{24} microbial cells.[47,48] It plays a fundamental role in shaping the Earth's microbiome, both as a global transport medium and as a habitat for microbially mediated processes, including ice nucleation and chemical transformations.[47–49] Airborne microorganisms influence air quality, weather, global climate, and the health of organisms, including humans.[50,51] Evidence suggests that microorganisms attached to substrates gain survival advantages during dispersal,[48] and consequently, the majority of airborne microorganisms are particle bound rather than free floating.[48,52–55] As an emerging and ubiquitous form of airborne PM, microplastics serve as important binding sites for microorganisms, potentially leading to ecological and human health impacts—a topic that has largely been overlooked. Indeed, emerging evidence has already shown linkages between microplastics and microorganisms in air.[28,56–58]

Plastic, as a novel, anthropogenic entity, did not exist on Earth prior to the Anthropocene, and microplastics, of course, were previously absent from the air.[5,59,60] Today, however, these particles have become globally pervasive, representing a new dimension of planetary-scale change and introducing complex, compounding impacts on a wide range of ecosystem types.[15,31] Furthermore, microplastic emissions are expected to increase over time[2,14] due to growth in plastic production, leakage of plastics into the environment, persistence and slow, if any, degradation, and fragmentation of existing environmental plastics.[61] This suggests that the burden of microplastics in the atmosphere will increase, and their associated impacts are likely to be amplified in the future. However, a predictive understanding of the impacts of airborne microplastics via interactions with airborne microorganisms remains lacking.

In this review, we therefore aim to disentangle the complexities of the airborne plastisphere and identify overlooked impacts, which is essential to gain a more comprehensive understanding of the risks of plastic pollution and to inform policymakers with science-based evidence. Since there are no formal definitions yet, and because the plastisphere occurring in different ecosystem compartments faces distinct ambient conditions and biogeochemical and microbial cycling dynamics, we define the airborne plastisphere as "the ecosystem composed of airborne plastic and its inhabiting microbiome." Building on this definition, we identify the characteristics of airborne microplastics that are relevant to microbial attachment and colonization, and we evaluate potential threats posed by the airborne plastisphere. We show that microplastics are expected to support a disproportionately high microbial biomass, increase airborne concentrations of active microbial components, and alter the structure of airborne microbial communities. Overall, the ongoing increase in microplastics in air and their capacity to support, transport, and interact with microorganisms pose escalating threats to planetary health.

CURRENT KNOWLEDGE OF PLASTISPHERE MICROBIOLOGY

Development of research on plastisphere microbiology

The term "plastisphere" was first proposed in 2013 to describe the microbial community living on marine plastic debris.[62] This sparked numerous studies on plastic-associated microbial communities, and a related knowledge framework was rapidly developed. Similar to the trajectory of microplastic research, studies of the plastisphere also began in aquatic ecosystems, expanded to soil ecosystems, and only recently included the largely unexplored atmospheric compartment. Over time, the definition of the plastisphere has evolved.[36] The term "plastisphere" was initially used to refer specifically to microorganisms associated with plastics.[62] However, some researchers now also include the microenvironment created by plastics within the definition of the plastisphere, drawing an analogy with other "-spheres" such as the hydrosphere, atmosphere, rhizosphere, and phyllosphere.[36,37] The concept of the soil plastisphere, for example, has recently been redefined to encompass not only the plastic

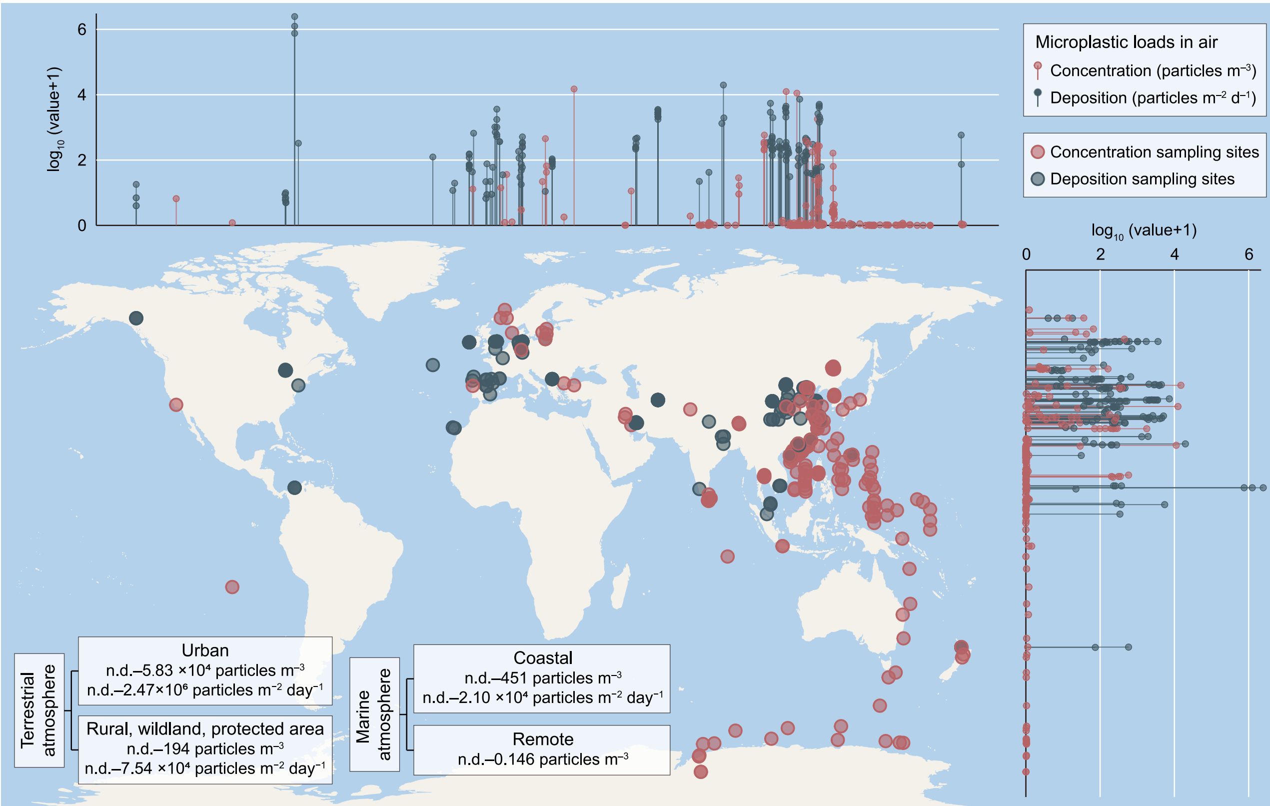

Figure 1. Summary of published surveys quantifying microplastic loads in air

Data indicate that microplastics are ubiquitous in the atmosphere even in protected land areas and above remote oceans. The dataset includes 92 peer-reviewed studies published since 2015 (see the methods section for detailed descriptions of data collection, processing methods, and the compiled dataset). The quantitative microplastic data were converted to common units (particles m^{-3} for samples from active sampling and particles m^{-2} day^{-1} for samples from passive sampling), but the sampling and analytical methods used in different studies were inconsistent due to a lack of standardized or harmonized sampling and analytical procedures, which limits comparability. Dot-line plots report airborne microplastic abundances at each site, with multiple points on one line indicating that there are multiple values at one site or at geographically close sampling sites. The numbers in the bottom-left boxes indicate the abundance ranges of airborne microplastics detected in different environmental compartments (n.d., not detected).

surface but also the soil environment influenced by plastics, as well as the microbial community that may not be directly attached to plastic but resides in plastic-affected soil.[36] However, defining the plastisphere in the atmosphere presents unique challenges. Unlike soil or aquatic environments, the atmosphere is characterized by fluid and rapid movements, making it difficult to form a stable, non-attached microenvironment with a steady microbial community. Therefore, the airborne plastisphere is likely limited to matter directly attached to airborne plastic particles. As a pioneering review of this emerging research area, we formally clarify the definition of the airborne plastisphere as "the ecosystem composed of airborne plastic and its inhabiting microbiome" (Figure 2). Notably, the microbiome does not refer just to the community of microorganisms but also includes the complete theater of activity, including structural elements (genes and proteins), metabolites and signal molecules, and the surrounding environmental conditions.[63,64] We emphasize that the chemical and biological components produced by airborne plastisphere microorganisms, such as endotoxins, mycotoxins, glucans, fungal spores, mobile genetic elements, and antibiotic-resistance genes, should also be considered, as these atmospheric components can have significant impacts on ecological and human health.[65–68] Plastic particles often have very small sizes, down to sizes commonly referred to as nanoplastics (<1 μm).[30,36,69] Although nano-sized plastic particles are not large enough to serve as habitats for microorganisms such as bacteria and fungi (which are typically larger), they can still be a vector for viruses, antibiotic-resistance genes, mobile genetic elements, and chemicals. For our purposes, therefore, we do not set a lower size limit for plastic particles that can constitute the plastisphere.

General pattern of microbial ecology in plastisphere

As a novel entity created by humans,[5] plastics provide a whole new niche for the Earth's microorganisms.[35,37] Consequently, microbial communities that assemble in the plastisphere typically have a composition and structure distinct from those found in natural habitats and on other particles.[37,42] This selective assembly of microorganisms has been well documented in aquatic and soil ecosystems,[33,36,37,70–72] and emerging evidence indicates similar patterns in the airborne plastisphere.[56] Consequently, plastisphere microbiomes typically exhibit distinct functional profiles.[37,72,73] For example, elemental biogeochemical functional potentials are altered in the plastisphere,[74–76] with

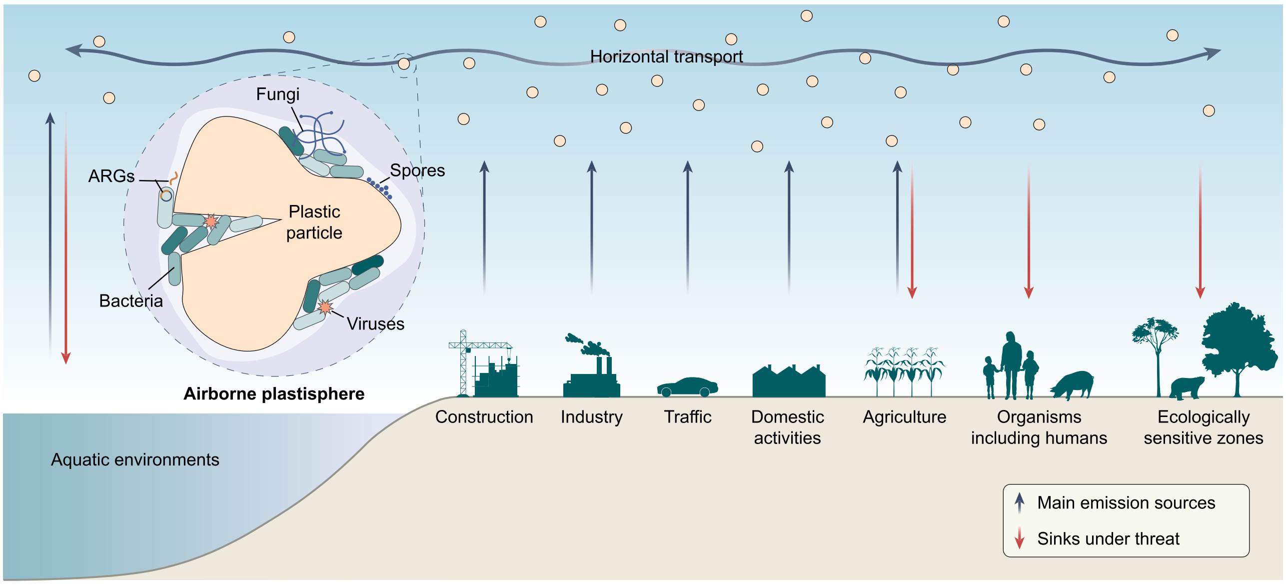

Figure 2. Microplastics and their associated microbiome in air
Pollution sources such as construction work, industrial processes, traffic, domestic activities, and agriculture continuously emit plastic particles into the atmosphere. These particles can carry microorganisms as well as their associated components such as spores and antibiotic-resistance genes (ARGs) into the atmosphere from aquatic or terrestrial environments or acquire them through contact in air. This microecosystem, in which plastic particles act as a matrix, is referred to as the airborne plastisphere. The deposition of microplastics together with their microbial colonizers and components could pose potential ecological and human health risks.

the organic carbon metabolic capacity generally enhanced in both the aquatic and the soil plastisphere (Figure 3), potentially influencing the biogeochemical processes of ecosystems.[35,37,72,77] However, the elemental biogeochemical potential in the airborne plastisphere and the associated ecological impact remain critical knowledge gaps (see detailed discussion in the section "the airborne plastisphere and ecological impacts"). Pathogens and antibiotic-resistance genes are commonly enriched in the plastisphere (Figure 3), posing significant potential health threats to biota, including humans.[35–37,78] This phenomenon has been extensively documented in aquatic and soil ecosystems,[39,41,45,72,79] and emerging evidence also points to similar risks in air[28,56,80] (see detailed discussion in the section "the airborne plastisphere and One Health risks").

Differences across ecosystem compartments

In soil, the plastisphere may not offer significant advantages in terms of supporting microbial biomass, as soil itself is already rich in particles and nutrients (Figure 3). In contrast, in aquatic ecosystems—particularly in harsh environments or nutrient-poor areas such as the open ocean—the plastisphere often acts as a shelter protecting microorganisms from external stressors and providing carbon sources and nutrients.[33,35,38,81–83] Furthermore, most microorganisms prefer attached surfaces to a free-living lifestyle, often resulting in substantial microbial biomass colonizing the plastisphere in aquatic ecosystems (Figure 3).[33,84] But what about the situation in air, a habitat characterized by high stresses and harsh conditions? The shelter role should be enhanced (see detailed discussion in the section "plastisphere microenvironment enhances microbial survival"). Another key difference in the plastisphere across ecosystem compartments is mobility. Plastic debris in soil, particularly such that enters the interior of the soil, tends to become trapped by the surrounding material, resulting in low mobility (Figure 3). This limited movement allows the plastisphere in soil to interact extensively with its surroundings, leading to relatively stable microbial community structures influenced by localized microscale processes.[36] The soil plastisphere often has a lower microbial diversity than the surrounding bulk soil due to selective assembly from the surrounding species pool.[36,72] In aquatic environments, plastic debris is transported vertically and horizontally by currents, as well as among and within food webs, which creates highly dynamic microbial communities that change in response to fluctuating environmental conditions.[81] As the plastisphere provides shelter, some microbial species can be transported from their source/upstream habitats, contributing to the higher species richness often observed in the aquatic plastisphere compared to the surrounding water.[42,82] Due to its mobility and protective role, the plastisphere in aquatic environments poses a heightened risk of facilitating microbial invasions (Figure 3).[35,38,42,82] In the atmosphere, plastics harboring microorganisms are continuously moved by airflow, thereby potentially exacerbating the risk of microbial invasions.

TRAITS OF MICROPLASTICS AS A MICROBIAL HABITAT IN AIR

Microorganisms transport from source environments to air

Plastic particles can easily be released into the atmosphere from the Earth's surface, including from terrestrial and marine ecosystems[85,86] (Figure 2), in particular following weathering of plastic items due to a diverse set of factors including UV light, biological

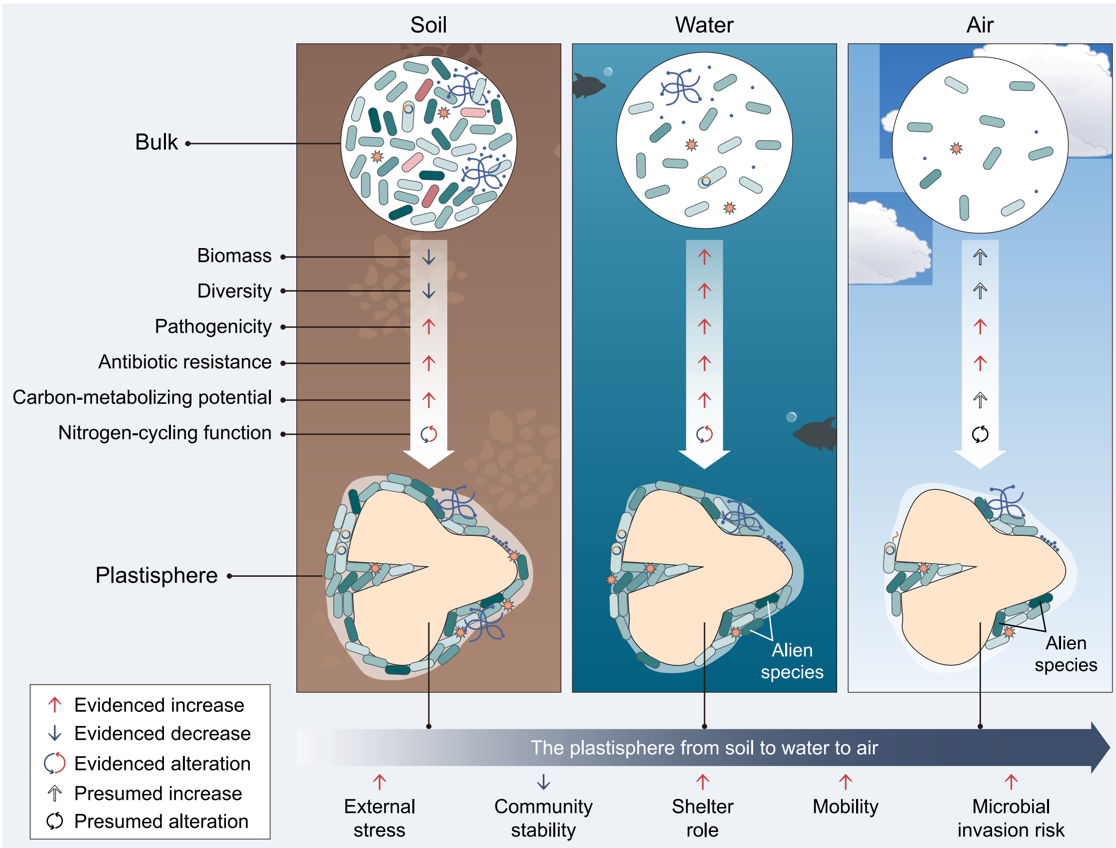

Figure 3. Current knowledge about the plastisphere in soil, water, and air
Relative to bulk soil, soil plastisphere communities typically show decreased biomass and diversity; increased pathogenicity, antibiotic resistance, and carbon-metabolizing potential; and altered nitrogen-cycling functions. Relative to bulk water, aquatic plastisphere communities generally exhibit increased biomass, diversity, pathogenicity, and antibiotic resistance; elevated carbon-metabolizing potential; and altered nitrogen-cycling functions. In air, compared with the surrounding aerosol microbiome, the airborne plastisphere has been shown to harbor increased pathogenicity and antibiotic resistance; increases in biomass, diversity, and carbon-metabolizing potential are inferred, and nitrogen-cycling functions are likely altered. From soil to water to air, the external stress, shelter role, mobility, and microbial invasion risk of the plastisphere are expected to increase, whereas the stability of plastisphere communities tends to decrease.

degradation, mechanical stress, and changing temperatures.[18,87] In terrestrial ecosystems, airborne microplastics originate primarily from industrial and agricultural activities, construction work, urban dust, synthetic textiles, weathered plastic waste, and automobile tire and brake wear.[85,88–91] It is estimated that approximately 48 kT of microplastics are released from global soil ecosystems into the atmosphere per year.[85] In marine systems, microplastics can be emitted and transported into the atmosphere via sea spray aerosols,[86,89,92–94] and it is estimated that globally >1 kT of microplastics is emitted from the ocean surface into the atmosphere each year.[86]

Unlike many airborne types of PM, especially fine particles (<2.5 μm), that can be emitted directly through combustion or formed in the atmosphere,[95] microplastics cannot be formed directly in air and mainly originate from non-combustion sources.[96] For example, airborne microplastics in the western United States were estimated to be primarily derived from reemission sources: roads (84%), the ocean (11%), and agricultural soil dust (5%).[96] As such, airborne microplastics can carry microorganisms from their source environmental compartments, such as water and soil, into the atmosphere, as they are not subjected to high temperatures that can destroy biological matter (Figure 4). Once airborne, microplastics could also interact with microorganisms in air via random collisions, as other airborne PM does (Figure 4).

Long atmospheric residence time and transport distance

Airborne plastics are estimated to have atmospheric residence times ranging from days to weeks, comparable to fine particles and far longer than many other types of aerosols of similar size.[96–98] For example, the atmospheric lifetime of global sea salt aerosols is estimated to be a few hours[99]; the atmospheric lifetime of tire and brake microplastics in the $PM_{2.5}$ size mode is about 4 weeks,[97] while that of similarly sized black carbon aerosols is about 1 week.[100] Once airborne, microplastics can travel long distances rapidly, even crossing continents or hemispheres.[20,101,102] For example, high-altitude measurements have detected plastic fibers and fragments in the free troposphere, indicating long-range transport from their sources.[103,104] Likewise, microplastics have been collected in remote regions, such as remote mountain ranges and polar marine environments, as well as isolated, protected areas, providing multiple lines of evidence for long-range, atmospheric transport over thousands of kilometers.[20,24,30,105]

Compared to typical airborne PM, the low density, highly irregular shape, hydrophobicity, insolubility, and durability of microplastics facilitate their extended atmospheric residence time and long-range transport. The density of airborne microplastics is typically between 0.8 and 1.4 g cm^{-3} (often around 1 g cm^{-3}),[22,34] which is significantly lower than that of many other types of aerosols, such as dust (around 2.65 g cm^{-3}), metals, and salts.[20,34,85,103] This lower density often results in the aerodynamic drag force substantially exceeding gravitational forces, allowing microplastics to remain suspended and transported horizontally or vertically with airflow, rather than settling.[22,95,96,106,107] Particles smaller than a certain critical size (presumed to be 3–4 μm for dust) have a preference to disperse to downwind areas.[108] The lower density of microplastics indicates a larger critical size threshold or a longer transport distance compared to denser aerosols of similar sizes. Furthermore, microplastics are in many cases fibrous or irregular fragments rather than compact spheres. Irregular shapes typically experience higher aerodynamic drag and have a smaller aerodynamic diameter than equal-volume spheres, which also slows their settling.[20,106,109,110] The hydrophobic and insoluble surfaces of microplastics also decrease their likelihood of becoming waterlogged or dissolving, potentially limiting their capacity to nucleate cloud droplets and thereby potentially reducing their wet deposition.[22,97] In addition, following initial deposition, the durability and persistence of microplastics enable them to continuously cycle between the air and the aquatic and/or terrestrial realm, becoming resuspended in the air, facilitating further transport.[89,111]

Therefore, beyond carrying microorganisms from source environments into the atmosphere, the long atmospheric lifetimes and transport distances of microplastics increase the likelihood of encounters between microplastics and airborne microorganisms via random collisions, potentially enhancing microplastic-microorganism interactions. Additionally, the attachment of microorganisms to microplastics with lower densities than many other types of PM may enhance atmospheric residence times of these microbe hitchhikers in the atmosphere or leave them less impacted, whereas attachment of microbes to PM with higher densities accelerates the sinking of microorganisms along with these airborne particles.[48] Therefore, microplastics potentially serve as aerial rafts, keeping microbes aloft for longer and facilitating their wider dispersal and more sustained interactions in the atmosphere (Figure 4).

Sufficient surface area for microbial attachment

Because of their slow settling discussed in the last section, collectively, microplastics suspended in air are generally larger than many other airborne particles.[22] For example, microplastics measuring hundreds of micrometers can have settling velocities similar to those of typical submicrometer particles.[105] Field measurements have shown that microplastic particles ranging from hundreds to thousands of micrometers in size (e.g., millimeter scale) are common in the atmosphere.[22,24,30,85,86,92,109,112] Even after traveling long distances to remote areas, microplastics of the size of dozens of micrometers remain prevalent.[103,113] These sizes are orders of magnitude larger than typical atmospheric aerosols, such as sulfates, soot, or clay dust, which usually have diameters <10 μm and often <2.5 μm.[22]

The larger size of microplastics provides a greater surface area for microorganisms to attach to and colonize (Figure 4). For example, a 100-μm microplastic fragment has a surface area thousands of times greater than that of a typical 1- to 2-μm aerosol particle, with the potential to accommodate thousands of microbial cells (mostly with body sizes around 1 μm[114]). Even elongated microplastic fibers, usually ∼10–20 μm wide and much longer,[109] provide ample surface area for hundreds of microorganisms. Additionally, the large surface area of airborne microplastics allows multiple layers of microorganisms to attach, contributing to biofilm formation. Weathering processes can also create rough textures, cracks, and pores on microplastic surfaces, further increasing their specific surface area[101] and enhancing their potential to carry microbial biomass.

Plastisphere microenvironment enhances microbial survival

In general, microorganisms, including pathogens and viruses, can easily be transmitted in aerosols over short distances, for instance, person-to-person transmissions.[48] However, without protection against environmental stressors, microorganisms can quickly become inactivated due to atmospheric stressors, which may impede long-range dispersal.[48]

Microplastics, as a type of inert carbon,[15] readily adsorb organic matter onto their surfaces and thus can create a relatively nutrient-rich, benign microenvironment for microbial colonization (Figure 4).[33,83,115,116] Holes and cracks in the surface of microplastics provide shelter for microorganisms and reduce their exposure to external stressors.[82] The rough, organic surface of microplastics facilitates attachment of microbial secretions, such as extracellular polysaccharides, and biofilm formation (Figure 4).[36] These biofilms, in turn, help protect microorganisms from harsh environmental conditions.[117] Therefore, microorganisms can rapidly colonize plastic surfaces in the environment, which may enhance their survival and growth.[118] In harsh or nutrient-poor environments, such as open oceanic systems, the plastisphere often acts as a nutrient island and thus harbors significantly higher microbial biomass compared to the surrounding environment.[33,38] For example, it has been estimated that 1 g of marine plastic debris can carry 10 times more microbial biomass than 1,000 L of water from the open ocean.[118] The plastisphere may also help to buffer environmental stress on microorganisms, for example, its demonstrated sheltering role during the transition from fresh water to seawater.[81,82] The plastisphere's ability to prolong the survival and infectivity of microorganisms, including pathogens and viruses, is also well documented.[35,38,43,45,78]

The atmosphere is characterized by low moisture and nutrient contents and high UV and ozone stress, which makes it inhospitable to microorganisms.[48] In such hostile environments, microplastics likely serve as fragmented refuges, providing microorganisms with habitats, protection, and nutrients, thereby enhancing their survival and potentially extending their dispersal range in the atmosphere (Figure 4).

Overall, the combined characteristics of their sources, their physicochemical properties, and their fate and transport make airborne microplastics an important class of airborne PM in terms of interaction with and support of microorganisms (Figure 4). Given

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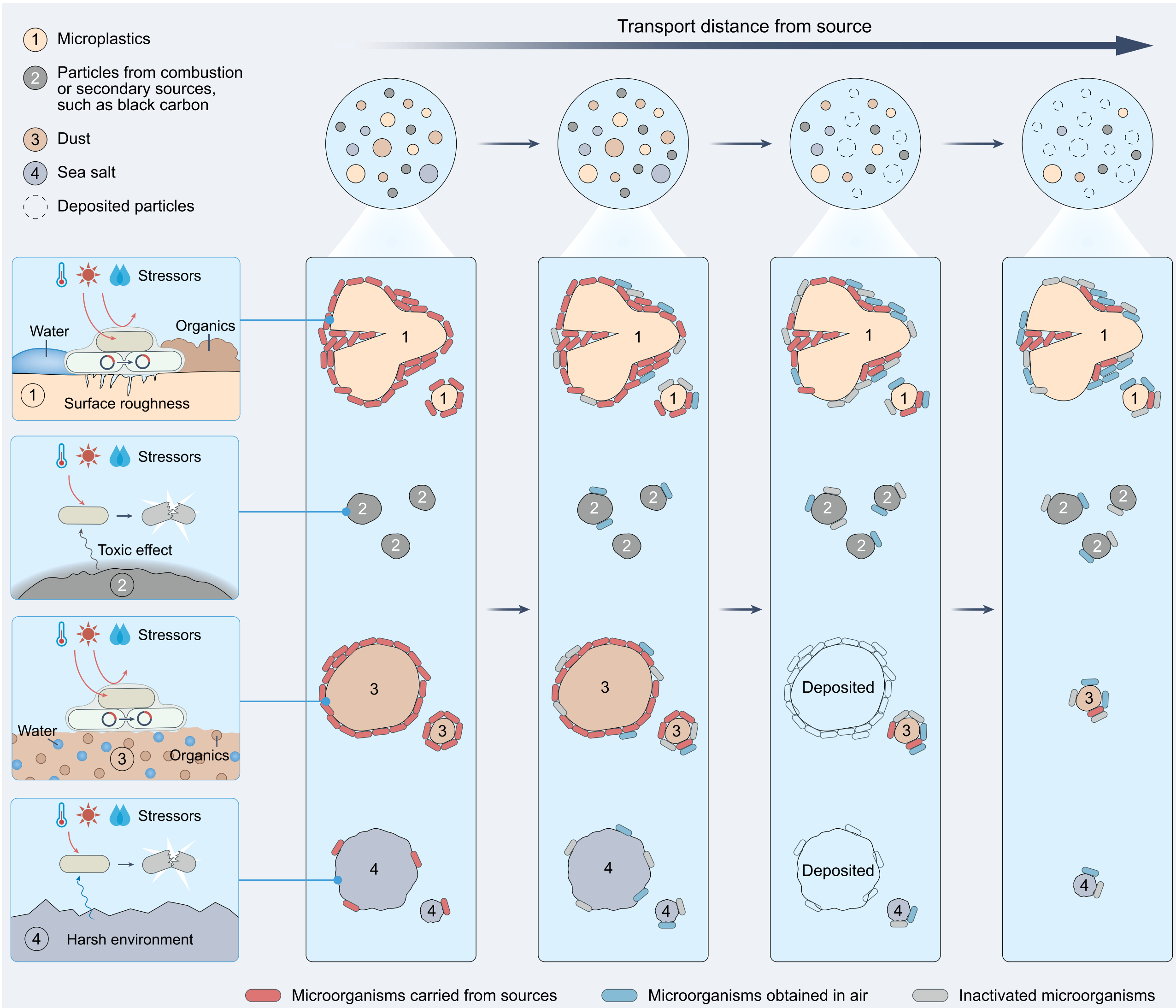

Figure 4. Hypothesized mechanisms of microplastics as a key habitat for microorganisms in the atmosphere
From a source perspective, unlike particles from combustion or secondary sources such as black carbon, airborne microplastics are primarily particles that largely bypass the high-temperature combustion processes that eliminate various forms of life. This allows microplastics to carry microorganisms from their source habitats into the atmosphere. From a physical perspective, compared to other particles from non-combustion sources such as dust and sea salts, microplastics are typically characterized by a lower density, irregular shape, and greater persistence. These properties could enhance the capacity of microorganisms for long-term residence and long-range transport in the atmosphere. From a chemical perspective, many particles such as black carbon and sea salt do not provide nutrition for microorganisms but rather cause toxic effects and impose stress on them. Furthermore, the adhesion of organic matter and moisture and the formation of biofilms on the surface of microplastics could protect microorganisms from harsh environmental stresses in air, such as low temperatures, high levels of UV radiation, and a lack of moisture.

that a substantial proportion of airborne microorganisms are particle attached,[52–54] and that microplastics are becoming increasingly prevalent airborne PM,[20,26,30] coupled with the enhanced capacity of microplastics to interact with and support the growth of microorganisms, airborne microplastics are expected to play an important role in shaping these microbial communities.

POTENTIAL IMPACTS OF THE AIRBORNE PLASTISPHERE

The airborne plastisphere may have significant direct and indirect impacts on Earth systems, since (1) airborne microorganisms influence air quality, weather, global climate, and biological health[48,50,51]; (2) many airborne microorganisms are particle attached[48,52–54]; and (3) airborne microplastics potentially have an enhanced capability of carrying, supporting, and interacting with airborne microorganisms for long time periods with corresponding long transport distances. As the concentration of microplastics in the atmosphere is expected to increase in the future, so too may their potential impact on airborne microorganisms, along with the related risks to environmental and human health. The next sections discuss the potential risks of the airborne plastisphere from both ecological and human health perspectives in order to

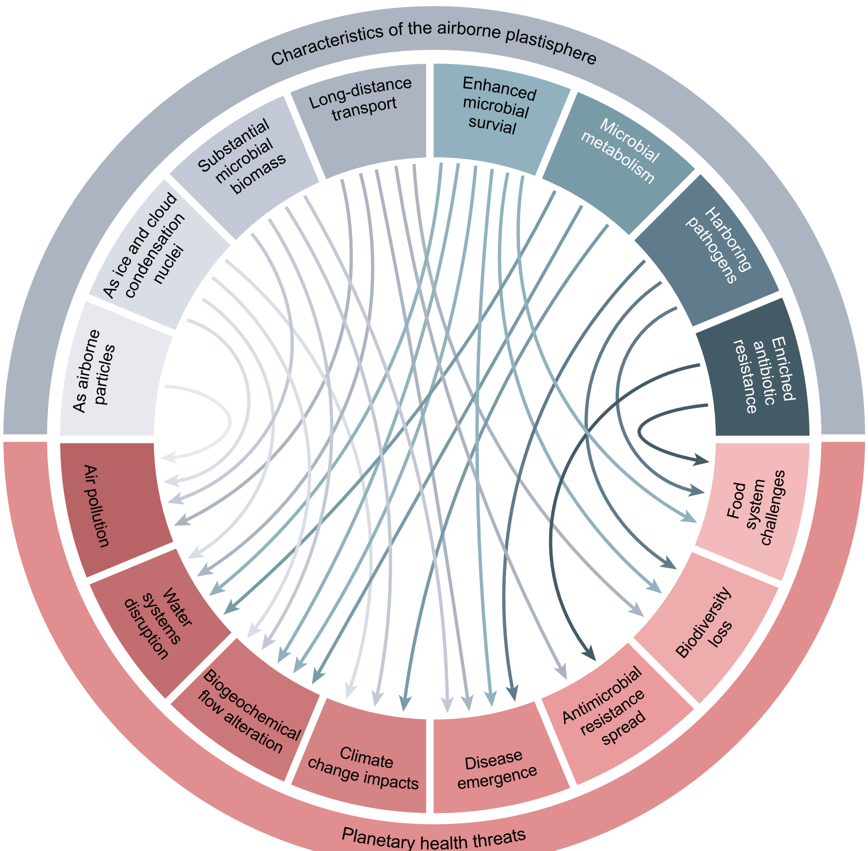

Figure 5. Planetary health threats associated with airborne plastisphere characteristics

The upper semicircle summarizes eight defining characteristics of the airborne plastisphere; the lower semicircle summarizes eight planetary health threat domains. Arrows link specific characteristics to the threat domains they may influence, indicating hypothesized pathways of impact.

inform risk assessments and establish a clear call for science-based action.

The airborne plastisphere and ecological impacts

Patterns of microbial biogeography suggest that the aerosolization and transport of microorganisms are crucial for species dispersal between ecosystem compartments and for the assembly of local microbial communities.[48,119] In this case, given the long-range transportability of airborne microplastics coupled with their protective effect on the attached microorganisms, the emergence and enhancement of the airborne plastisphere may expand the dispersal scale of these microorganisms. This mechanism could disrupt the structure and function of microbial ecological communities and affect biodiversity not only in the atmosphere but also in aquatic and terrestrial ecosystems where they are eventually deposited (Figure 5). The potential consequences include increased homogenization of microbial distributions across geographical regions, an increased risk of microbial invasions, the spread of disease, and ecosystem-wide ecological impacts such as harmful algal blooms (Figure 5).[48,120]

Microplastics can reach remote and wilderness areas.[20,24,88,89,96,97,103,121,122] For example, >1,000 tons of plastics are estimated to fall on national parks and wilderness areas in the western United States each year.[20] Microplastics can be transported through the atmosphere and deposited in areas such as the remote open ocean,[30,105] polar regions,[9,88,97,113] and mountainous regions such as the Tibetan Plateau, the Andes, or the Alps.[20,104,113,121,122] These areas typically are ecologically vulnerable, being less resilient to external disturbances, but play a critical role in maintaining planetary health. If plastic particles carrying microorganisms enter these ecosystems, the dynamics of local microbial communities and ecological processes could be altered or disrupted,[105] and correspondingly, negative cascading effects on biodiversity and the structure, function, and services of ecosystems could occur (Figure 5).

Since the airborne plastisphere potentially has an enhanced capacity of harboring microbial biomass and supporting microbial growth and survival, an increase in the abundance of microorganisms and their components in air is expected as airborne microplastic concentrations increase. This conclusion is supported by recent observations of significant positive correlations between airborne microbial concentrations and airborne microplastics.[57,58]

Microbial cells and many of their components in air can act as ice and cloud condensation nuclei, thus driving cloud formation processes.[123,124] Due to the inherent hydrophobicity of many plastic particles, they were initially considered to be inactive cloud condensation nuclei but are likely to be active ice-nucleating particles.[22,125] However, the weathering processes, either in the atmosphere or in terrestrial or aquatic systems before their (re)suspension, can alter their chemical composition and increase their affinity to water.[89] Additionally, the adhesion of natural or anthropogenic chemicals onto airborne microplastic surfaces can increase their colonization potential and wettability.[89] These processes allow plastic particles to function as cloud condensation nuclei.[89] Although their current impact on cloud formation processes may be very limited, the increasing concentration of airborne microplastics demands recognition of their spiraling impacts. Overall, both the airborne plastisphere and the microbial cells (and their components) that are scattered from the plastisphere during transport may contribute to cloud formation processes. This could potentially affect the weather and precipitation, causing non-negligible climate perturbations, especially in sensitive, pristine, and remote ecosystems[89] or highly polluted areas (Figure 5).

Airborne microorganisms also have the potential to affect biogeochemical processes through metabolic activities such as carbon fixation or degradation of carbon compounds.[48] The airborne plastisphere potentially harbors a substantial proportion of airborne microorganisms; thus, some biogeochemical processes may be impacted (Figure 5). Metabolic activities related to biogeochemical processes could be enhanced within the airborne plastisphere, and the plastisphere is a potential hotspot for microorganisms as well as a site where organic compounds that are potential substrates for microbial metabolism are sorbed.[77,115,116,126] This has been demonstrated by an increased microbial capacity to metabolize organic compounds within the plastisphere in aquatic and terrestrial ecosystems.[37,77,126]

The airborne plastisphere and One Health risks

The plastisphere in aquatic and terrestrial ecosystems is generally enriched with harmful microorganisms and genes, including potential pathogens, virulence factors, viruses, and antibiotic-resistance genes, compared to the surrounding environment.[33,36–38,41,43,45,82,127,128] Several factors contribute to this pattern. First, surface defects and roughness of microplastics, especially after weathering, facilitate the adhesion of extracellular polysaccharides and other adhesins secreted by microorganisms, forming biofilms.[36,38,129] Many pathogens are biofilm associated, so they may initiate their colonization first and then gain a competitive advantage through biofilm formation.[36,38] Biofilms, in which cells are tightly attached to one another, increasing the opportunity for horizontal gene transfer among microorganisms, can lead to an increase in the abundance of antibiotic-resistance genes.[130–132] In addition, plastisphere microenvironments are often enriched with pollutants, such as antibiotics[133] and heavy metals,[134] which exerts selection pressure on antibiotic-resistance genes.[135,136] Furthermore, some microplastics may originate from, or travel through, hotspots of critical health-related environmental zones, such as wastewater treatment plants,[137] hospitals,[138] landfills,[139] livestock farms and other agricultural areas,[140–142] and aquaculture sites.[143,144] They may therefore carry harmful microorganisms and genes from these hotspots into new habitats.

The factors that facilitate the growth of disease-causing agents and harmful genes in the aquatic and terrestrial plastisphere may also apply to the airborne plastisphere. Therefore, the airborne plastisphere may also act as a mobile hotspot of health-related agents, including pathogens, viruses, and antibiotic-resistance genes. This conclusion is strongly supported by recent studies showing positive correlations between quantities of microplastics in airborne PM or dust and the status of pathogenicity,[28] SARS-CoV-2,[80] and antibiotic-resistance genes.[56]

Furthermore, since microbes are expected to be sheltered from hostile environmental influences when inhabiting the airborne plastisphere, the survival time and potential transmission of disease-causing agents in the air would increase, as the ability of the plastisphere to prolong the survival and infectivity of microbes has been demonstrated even in environments largely free of environmental stress and nutrient limitation.[38,43,128] This ability has the potential to increase the concentration of active pathogens and viruses in the atmosphere.

As a result, the load of health-related agents in the atmosphere may increase as the concentration of airborne microplastics rises. These health-related agents may be spread over greater distances by airborne microplastics with long-distance transport capacities (Figure 5). Finally, the health risks for all organisms, including diseases, allergies, and antimicrobial resistance, could increase (Figure 5) with deposition of airborne microplastics together with their microbial residents on the skin of animals and humans[145] or plant surfaces such as the phyllosphere[146,147] or via inhalation.[148,149] The One Health principle emphasizes that human welfare, biodiversity, and ecosystem health are inherently interconnected.[67,150–152] Therefore, even airborne microplastics and their harmful microbial residents that do not interact with organisms directly can cause subsequent, indirect health consequences due to increased concentrations and expanded transmission of microbial hazards in the environment. Overall, the airborne plastisphere may exacerbate the microbiology-related health risks associated with air pollution.[153–155]

FUTURE RESEARCH OPPORTUNITIES AND RECOMMENDATIONS

There is a growing awareness of the importance of adopting a planetary health perspective in order to understand the characteristics, impacts, and corresponding underlying mechanisms of the airborne plastisphere. Achieving this understanding requires joint efforts of scientists from various disciplines, including atmospheric sciences and modeling, microbiology, ecotoxicology, environmental (biogeo)chemistry, public health, and data science. A clearer understanding can then be used to develop, refine, and present potential risk mitigation strategies to policymakers and society, informing evidence-based, science-oriented approaches to counteract these potential threats. Given the large knowledge gaps within this broad topic, we offer ideas and recommendations to support future research and development of this emerging field.

General considerations on experimental design

If researchers intend to obtain direct evidence of the patterns and processes of the airborne plastisphere through laboratory simulation experiments, the following three core aspects should be considered when designing their experiments:

(1) Small particle size of airborne microplastics. Typically, the size of plastic fragments is not considered to have a significant effect on the structure of microbial communities when the habitat area is large enough to support many microorganisms. Therefore, larger plastic fragments are often used in studies on the aquatic or soil plastisphere. However, for airborne microplastic particles, the largest relevant size is in the millimeter range. A mature and stable microbial community that would form in larger habitats may not be established due to limitations in the available space. Therefore, we recommend that researchers use environmentally relevant sizes of airborne microplastics to adequately reflect the airborne plastisphere.
(2) Free-floating state of microplastics in air. A distinctive feature of airborne microplastics, compared to those in aquatic or soil environments, is that they exist predominantly as discrete, freely suspended particles rapidly moving with airflow. Aggregating or stacking microplastics within experimental containers instead of allowing

them to remain freely suspended alters the physicochemical conditions surrounding the airborne plastisphere, thereby influencing microbial colonization, evolution, and dispersal processes. Researchers are thus encouraged to adopt experimental designs that closely simulate the realistic, free-floating state of airborne microplastics.

(3) The complexity of microplastic pollution. Airborne microplastics are a complex mixture of particles with diverse sizes, shapes, polymers, additive compositions and levels, aging and weathering status, and associated matters, including sorbed chemicals and microbes, as captured and emphasized by the "microplastome" concept.[32] All these factors could exert significant impacts on the assembly of microbial communities and the associated function profiles.[41,73,79,156,157] Additionally, different environments usually face different conditions of microplastic pollution, e.g., different concentrations and different combinations of microplastic types.[10,32] Therefore, the complexity of microplastic contamination should be considered and simulated in the experiments.

Directly capturing the airborne plastisphere

Current sampling and analytical methods for airborne microplastics involve active or passive collection of all airborne PM, followed by isolation of microplastic particles through processes such as density separation, digestion, and filtration.[90,158] However, these processes usually destroy microorganisms, which makes further analysis of the plastisphere impossible. This challenge is likely the primary obstacle limiting the advancement of airborne plastisphere research.

To overcome this obstacle and capture the microbial ecology of the airborne plastisphere, developing specifically designed experimental chambers is necessary. Well-established chambers in the field of aerosol science could be adapted for airborne plastisphere research. For example, the ChAMBRe can grow, inject, and extract microorganisms within the chamber while preserving their viability for use in aerosol modeling and bioaerosol research.[159,160] Rotating drums, which are also often used for bioaerosol research, can minimize loss of aerosols due to gravitational settling.[161,162] By injecting microplastics into a chamber containing model microorganisms or real air, we can study the direct impacts of airborne microplastics on the viability, abundance, and composition of airborne microorganisms (Figure 6). Size fractionation could be used to isolate airborne plastisphere samples. For example, microplastics larger than a certain size (e.g., >10 μm) could be injected into the chamber, while air could be filtered through a filter with a specific pore size (e.g., 2.5 μm) that removes larger particles but retains most microorganisms. At the end of the experiment, microplastics can be collected on filters to obtain plastisphere samples for microbial community analysis (Figure 6). State-of-the-art biotechnological methods can be employed for plastisphere microbial analysis, such as polymerase chain reaction (PCR)-based techniques (e.g., conventional and high-throughput quantitative PCR),[163,164] sequence-based omics (e.g., amplicon sequencing, metagenomics, metatranscriptomics, metaproteomics, and single-cell sequencing),[37,165,166] isolation and cultivation,[167] and spectroscopic techniques (e.g., single-cell Raman spectroscopy[74,168]).

To obtain direct empirical evidence of the impacts of the airborne plastisphere on living organisms, controlled exposure experiments can be conducted on plants and/or animals. Building upon well-established air pollution exposure assays,[147,169,170] the impacts of the airborne plastisphere on model organisms can be determined by introducing airborne microplastics precoated with microorganisms (Figure 6). Techniques such as isotope labeling[74,168,171] and fluorescence labeling[147,172,173] offer robust methods to trace the uptake, distribution, and biological responses to these microplastic-associated entities. Given that airborne microplastics are in many cases persistent within host organisms and may elicit chronic cumulative physiological effects, extended-duration monitoring frameworks are essential to elucidate their ecological and health implications.

The characteristics and underlying drivers of the airborne plastisphere and its impact can be elucidated through controlled chamber experiments introducing diverse microplastic types varying in size, morphology, polymer composition, additives, and weathering state. Experimental designs incorporating comparisons with blanks and non-plastic aerosols such as sea salt, mineral dust, and black carbon can provide critical contrasts to isolate plastisphere-specific effects. Modifying abiotic conditions, such as light, humidity, and airflow, within the chamber enables one to assess how environmental factors influence the airborne plastisphere and its impacts. Conventional regression models and/or machine learning tools can be used to quantify and map the relationships between potential driving factors and airborne plastisphere microbial characteristics, including the associated impacts.[174] Once a model has been established, it is possible to predict airborne plastisphere microbial characteristics and their associated impacts using information on their potential driving factors. This will effectively address the challenge of obtaining airborne plastisphere microbial information in real environments.

Holistically assessing airborne plastisphere impacts

To better understand and assess the impacts of the airborne plastisphere in real-world conditions, a combination of data-driven analyses of real environmental samples and simulation-based experimental validation is recommended (Figure 6). Samples of airborne PM collected from different locations with varying land use (e.g., residential, industrial, rural, and protected areas) and different pollution statuses can be used to analyze the concentrations and type compositions of microplastics, as well as microbial information, across systems (Figure 6). Statistical tools such as redundancy analysis, mixed-effects models, and random forest models can then be used to identify associations between airborne microplastics and microbial characteristics (e.g., abundance, diversity, composition, function, and pathogenicity). Both airborne microorganisms and microplastics in the environment are influenced by a range of factors, including combined, complex interactions. Thus, complementary laboratory experiments are needed to corroborate the direct and indirect patterns as well as individual and combinational trends found in observation-based investigations.

Environmental and human health risk assessments of airborne microplastics using integrative approaches that consider physical, chemical, and microbiological effects are

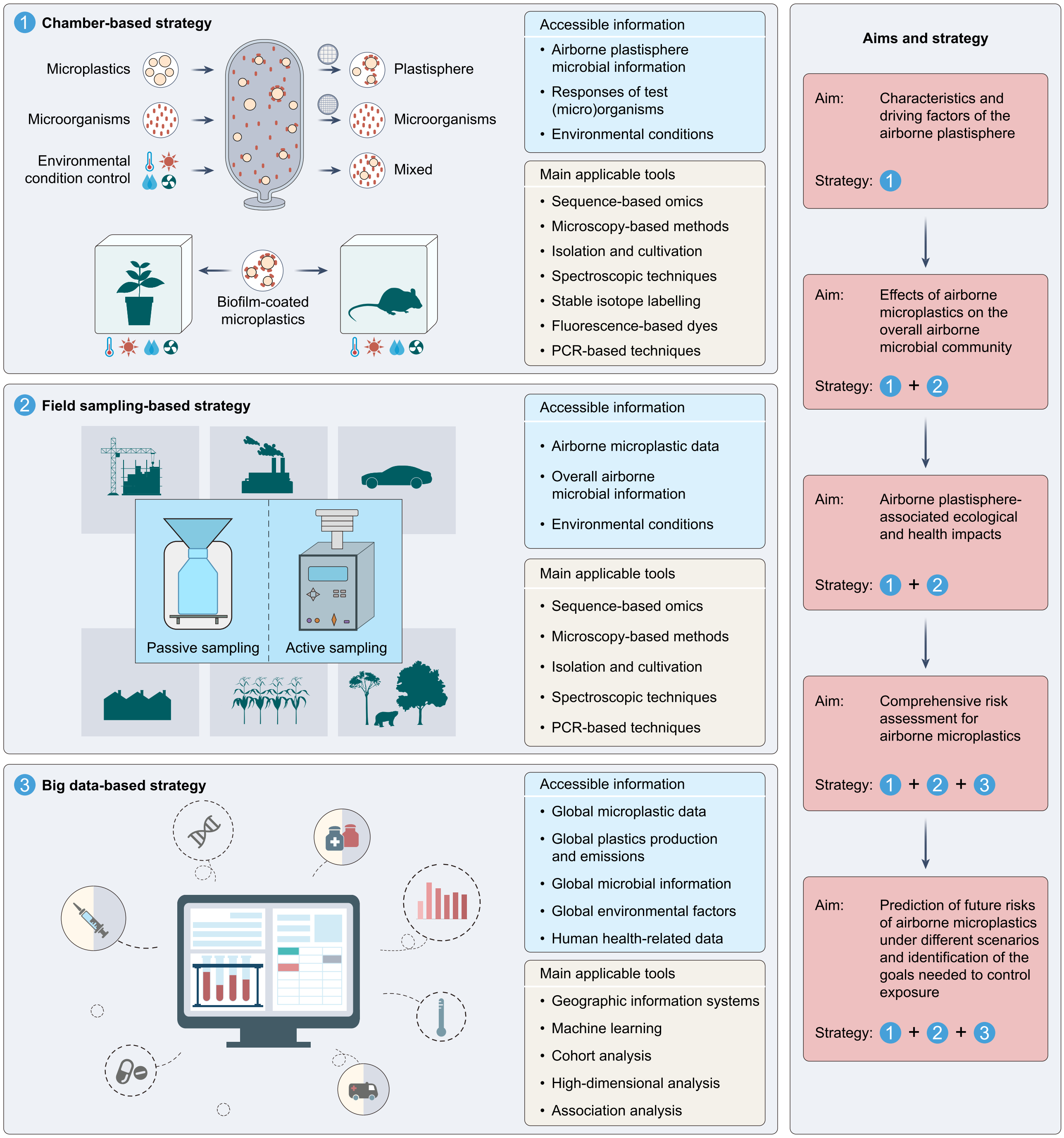

Figure 6. Future research opportunities
Potential research methodologies and strategies for exploring the ecology and impacts of the airborne plastisphere, comprehensively assessing and predicting risks of airborne microplastics, and informing effective management strategies.

crucial to gain a more comprehensive understanding of their potential threats. Therefore, ecotoxicological experiments on airborne microplastics should consider all three aspects individually and simultaneously. Data science can be utilized to investigate the relationship between airborne microplastic pollution and potential environmental or health events, such as the extent of microbial transmission, microbial-mediated ecological disturbances (e.g., algal blooms or disease outbreaks), and the spread of disease and antimicrobial resistance, by integrating and synthesizing observation-based data (Figure 6). A risk threshold for airborne microplastics should be established based on scientific evidence. Since different species, communities, and ecosystems have varying sensitivities to airborne microplastics, the risk threshold needs to be determined according to local environmental conditions, vulnerabilities, and requirements in order to ensure that it provides adequate protection.

It is particularly important to conduct risk assessments for airborne microplastics in areas of concern, such as urban areas, ecological reserves, Earth's critical zones, and ecologically vulnerable areas. Countermeasures should be developed to mitigate the adverse impacts of airborne microplastics in areas identified as high risk. Tools such as association analyses could be used to model the overall risk of airborne microplastics and their potential external drivers (e.g., plastic production and emissions as well as environmental conditions) (Figure 6). Then, the risk of airborne microplastics could be predicted under different future scenarios, for example, different levels of effort to promote the reduction of plastic production and circular-economy strategies, and different contexts, including other factors of global environmental change (e.g., increasing greenhouse gas concentrations, temperatures, and antimicrobial resistance). This would help to define the management goals needed to control exposure and minimize overall risk (Figure 6).

CONCLUDING REMARKS AND OUTLOOK

This paper discusses the emerging topic of the airborne plastisphere, examining its importance as a habitat and vector for airborne microbiomes as well as its potential impact on planetary health. The key message is that airborne microplastics may have far-reaching implications for planetary health due to their role in hosting airborne microbiomes, which can subsequently impact the entire airborne microbial community. This is especially concerning given that global plastic production and emissions are expected to increase substantially over the next decades unless global ambitious, effective management measures are established. We have identified research priorities and provided suggestions and ideas for future research, with the goal of promoting the advancement of this highly relevant new research field.

In the absence of direct evidence from real-world environments, this paper relies primarily on existing evidence from simulation experiments involving large plastic particles, as well as observed associations between airborne microplastics and microorganisms. We also draw on our understanding of the nature of plastic particles and their environmental behavioral characteristics as well as the patterns and transport dynamics of airborne microplastic pollution. We consider microbial ecology in heterogeneous environments and plastisphere microbiology in well-studied soil and aquatic ecosystems in order to make conservative inferences about the risks posed by airborne plastisphere microbiomes. Although the lack of sufficient direct evidence is a limitation, we have highlighted the potential risks that the airborne plastisphere could pose to planetary health. Furthermore, we demonstrate the importance of conducting research into this overlooked aspect of plastic pollution in order to stimulate future efforts and further exploration of this novel topic and thereby advance the field. This progress will eventually enable us to gather more science-based evidence, providing a comprehensive understanding of plastic pollution risks and informing the development of effective risk assessment and management strategies.

Last, many key questions regarding the primary, underlying mechanisms of this new topic remain unanswered. For example, what proportion of airborne microorganisms adhere to airborne microplastics? What fraction of the microbiome in the entire airborne plastisphere is carried into the air from the source systems of microplastics, and what fraction is acquired during atmospheric transport? How do the microbial communities in the airborne plastisphere and those carried from the source environments change during transport? How long and how far can microorganisms remain active after being carried from their source environments, and how important are reemission dynamics? What are the potential consequences and drivers of the interactions between airborne microorganisms and airborne chemicals such as black carbon, nitrogen oxides, and persistent organic pollutants in the plastisphere? The research ideas and recommendations that we have offered may also be useful for research, development, and capacity building in this area. In closing, further research is required to mitigate the ecological uncertainties and risks posed by the airborne plastisphere and to develop effective strategies to address these risks.

METHODS

To show evidence of plastic particles as an important component of airborne PM, we conducted a comprehensive literature review using the Web of Science (WoS) search engine. We searched with the query "TI=(microplastic OR microplastics OR plastic OR plastics) AND TI=(air OR airborne OR atmosphere OR atmospheric)". The resulting publications are compiled in the "Paper info" sheet of the "Global airborne microplastic dataset" Excel file (deposited at https://github.com/Changchao-Li/Airborne_plastisphere_threats). Publications prior to 2015 and those without a focus on airborne microplastics or not classified as research articles were manually excluded, resulting in a final dataset of 92 peer-reviewed papers. From these selected papers, we extracted the reported concentrations and/or deposition rates of airborne microplastics. All data were converted into standardized units (i.e., particles m^{-3} for samples from active sampling and particles m^{-2} day^{-1} for samples from passive sampling) to enable consistent comparisons across studies. In addition, we recorded various metadata for each study, including sampling locations, experimental design details, and sampling methods. All extracted data and associated details are compiled in the "Sample info" sheet of the dataset file. For sampling sites where explicit latitude and longitude coordinates were not provided, we estimated approximate locations based on maps or textual descriptions in the publications. We used the GetData Graph Digitizer software or Google Maps to derive coordinates in such cases. Finally, we compiled a consolidated dataset of airborne microplastic observations (see "Map data" sheet in the dataset file) and visualized these data on a global map (Figure 1) using R (version 4.2.2).

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AUTHOR CONTRIBUTIONS

C.L. proposed the initial concept and led the writing and revising, with L.N.J. and M.C.R. providing significant guidance, discussion, and editing. C.L. designed and drew all the diagrams. C.L., C.F., and T.Z. collected and organized the global airborne microplastic data. All other authors provided substantial professional insights, review, and editing from their respective areas of expertise, thus resulting in this interdisciplinary review.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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