REVIEW

Earth and Environmental Sciences

Bioaerosol nexus of air quality, climate system and human health

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Abstract: Aerosols of biological origins, known as bioaerosols, in addition to having the aerosol properties, have those of a living system that offers them some enabling functionalities. From science to technology, visible progress around the world has been made in bioaerosol field before and especially during the COVID-19 pandemic. Here the roles of bioaerosol across various disciplines, including air quality, climate and human health are highlighted and appreciated in light of Anthropocene and one health concept. In particular, we recognized the importance of aerobiology under haze air pollution, allergenic pollen and bioaerosol involvement in infectious and inflammation-related non-communicable diseases. Future interdisciplinary studies focusing on the chemical and biological process of microorganisms in air, airborne transmission of emerging pathogens and allergens and the association between bioaerosol exposure and the development and variations of human microbiome and immune response are needed to elucidate the interactions of bioaerosols with the earth system.

Keywords: bioaerosol, human health, climate change, air pollution

Overview

Various small living entities persist in the atmosphere due to their particle size ranging from tens of nanometers to tens of micrometers. Since the early observation of mold spores on the airborne dust particles by Charles Darwin (1833) from the Cape Verde islands, and the discovery of viable microorganisms by Louis Pasteur (1861), our knowledge on these small entities has been substantially improved [1]. As a vital component of atmospheric aerosols, these airborne microbes as well as their fragments are collectively referred to as bioaerosols. From the atmospheric science perspective, bioaerosols could affect the atmosphere in a manner similar to that of the intensely investigated chemical aerosols, e.g., atmospheric chemistry and climate. Yet bioaerosols differ from other chemical counterparts in that the majority of bioaerosols with intact cellular structure present life properties. Therefore, as a complex organic living entity, bioaerosols are also actively involved in the atmospheric processes. From the perspective of microbiology and immunology, bioaerosols, for instance, pathogenic microorganisms, antibiotic resistant microorganisms as well as their antibiotic resistant genes (ARGs), allergens, and even microorganisms as a whole, have direct health implications.

In the recent decade, high-throughput sequencing techniques have greatly boosted our understanding on the unseen microbial world. Together with other omics techniques, the roles of microorganisms on the health

of earth and humans have been unprecedentedly recognized. In this review, we aim to gain a latest understanding about the impacts of bioaerosols on earth system and public health.

To achieve this, we mainly searched the Web of Science database with the following keywords: "bioaerosol or aerobiology or PBAP or airborne bacteria or airborne fungi or airborne archaea or airborne endotoxin or airborne glucan or airborne microorganism or airborne microbiota or airborne microbiome" covering publications from Jan. 2016 to Oct. 2022. One reason we chose 2016 as a starting point is partly related to the comprehensive atmospheric bioaerosol review published in that year by Fröhlich-Nowoisky *et al.* [2]. In this previous review article, they mainly focused on the role of bioaerosols in the earth system, especially the interactions between bioaerosols and climate, health and ecosystem. Bioaerosol field is advancing very fast, including both science and technology. Since then, a wealth of advanced techniques has been applied to bioaerosol research field, which has greatly expanded our understanding on the bioaerosol taxonomy traits and some initial functional traits. Meanwhile, severe air pollution in China and other regions further stimulates studies on the correlation and interaction between bioaerosols and air pollutants. In face of the challenges from climate change, the characteristics and impacts of bioaerosols in the context of climate change have also been widely investigated, e.g., their IN/CCN (ice nuclei/cloud condensation nuclei) activity, allergenic potential. Moreover, the outbreak of COVID-19 (coronavirus disease 2019) highlighted the role of bioaerosols in human health. More than 6200 related publications were found using the keywords. Then, the occurrences and relationships among all keywords appearing in these publications were analyzed with VOSviewer. Figure 1 shows the network and frequencies of keywords appearing more than 150 times. These high frequency keywords were generally classified into three clusters. Before 2020, these bioaerosol papers mainly focused on their physical properties (e.g., size distribution) and microbial properties (e.g., identification, diversity, and communities) and their associations with particulate matter (PM), air pollution, and indoor air. From 2020, studies related to COVID-19 especially the number of studies regarding the transport and infectious of bioaerosols have increased sharply.

Overall, the cultivation-independent studies uncover a diversified airborne microbiome with a high re-
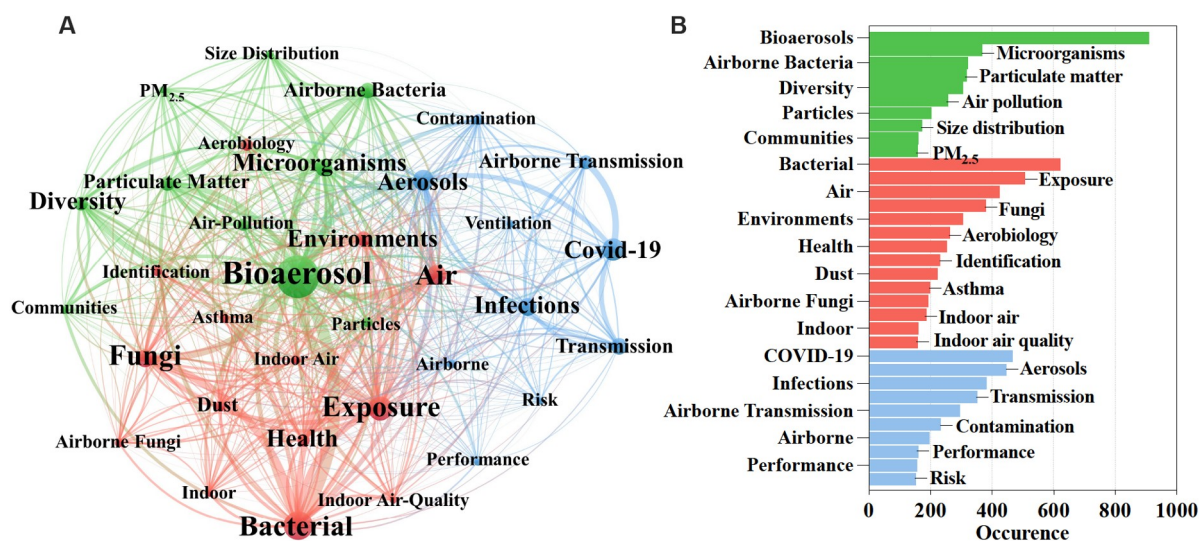

Figure 1 Bibliometric analysis of studies associated with bioaerosols from 2016 to 2022. (A) Network and (B) occurrences of keywords occurring more than 150 times in the bioaerosol-related publications (2016–2022). Color in the panel B corresponds to that in the panel A.

solution both spatially and temporally. The knowledge provides novel insights on the emission sources, transport, transformation and impact of bioaerosols in the areas including aerobiology under haze air pollution, allergy conditions, COVID-19 pandemic developments. Importantly, the role of bioaerosol across various disciplines, i.e., broadly air quality, climate system and human health, is more appreciated in this updated review, aiming to help further accelerate the bioaerosol research recognition and collaboration. Through the compilation of these updated information, we hope to promote bioaerosol study into next functional traits study phase to elucidate how the bioaerosols affect the health of earth and humans and to modulate the bioaerosols for the good of humans and the earth system.

Characteristics and dynamics of bioaerosols

Bioaerosols are suspended in the atmosphere in various forms, including free-floating single cells or cell aggregates, or attached onto other particles; and their debris or metabolites might also persist in the air in free-floating or attached form (Figure 2). This can be further inferred from the size distribution of bioaerosols studied with culture-independent methods, including DNA-based and fluorescence-based analysis. For instance, the average size of bacteria is 0.2–5 μm, and in the particles collected from the Sahara region, more than half of the bacterial DNA was detected in particles of larger than 10 μm [3], indicating a form of cell aggregates or attachment on larger particles. While in our previous fluorescence-based real-time observation in North China Plain, a size range peak of 2–3 and 1 μm or even lower were found for the urban site and the rural site, respectively [4]. With the single-particle mass spectrometry, around 30% to 80% of single bioaerosols were supposed to be in a mixture with dust [5]. In addition, the DNAs of fungi which are generally in a size range of 2–10 μm have also been detected in particles smaller than 1 μm [6], indicating that these fungal DNAs were likely released from dead fungi and existed in a free DNA form. In addition, using microscopic observation data, the particle-attached bacteria were found to account for more than 70% of the total airborne bacteria on dusty days, and 56%±17% on non-dusty days [7].

Benefiting from a variety of novel quantification and sequencing approaches, knowledge on the abundance
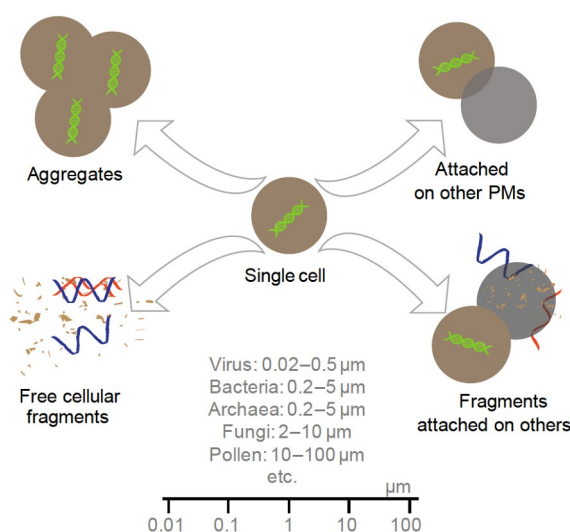
Figure 2 Physical characteristics of bioaerosols in the atmosphere.

and diversity of bioaerosols has greatly improved. Table 1 presents a snapshot of the airborne bacteria, fungi and pollen measured using non-culture methods around the world. Overall, the concentrations of bioaerosols in the atmosphere span from tens of to more than thousands of cells per cubic meter of air [8]. Despite the wide ranges of bacterial concentrations (10^1–10^8 gene copies/m^3), the variations among each continent and city are not significant, showing no clear trend. For instance, bacterial concentrations in the Sahara region were on a similar level with those in cities in Asia and Europe [3,9,10]. This similarity also appeared for fungi and pollen. On average, around 5×10^{22} bacteria exist in the global atmosphere, which is several magnitudes of order lower than those in the soil, ocean and phyllosphere [11]. A recent work updated this number of global airborne bacteria to be around 1.72×10^{24} cells [12]. And the amounts of archaea and fungi are usually lower than the bacterial counts [13]. Based on a modeling work, the annual fungal emission was in the range of 3.4–3.7 Tg/yr [14]. These bioaerosols serve as an important contributor to the airborne organic carbon, especially in the coarse particle ranges (up to 69%) [15].

Additionally, the atmospheric microbial community compositions were found to be as diverse as those of other ecosystems [33]. As shown in Table 1, the bacterial community was dominated by Proteobacteria, Firmicutes, Actinobacteria, Cyanobacteria, Bacteroidetes; and fungal community was dominated by Ascomycota and Basidiomycota. While for the pollen, their types varied with the locations.

Temporal variations of bioaerosol abundance and diversity

In a 13-yr long-term observation (2001–2013) over Chichijima island, data based on the sugar components (arabitol, mannitol, and trehalose) suggested an increasing trend of airborne microorganisms and pollen [34]. Another long-term data (1990–2018) in North America showed the increasing concentrations of airborne pollen [35]. Moreover, another long-term retrospective study presented that the increase of pollen abundance was also observed in various northern hemisphere sites [36].

In contrast to the increasing trend of bioaerosol abundance in recent decades, the bioaerosol diversity was found to be relatively stable in some sites. For instance, the fungal communities at Hawaii Island over the 13 years were relatively stable, with saprotrophs *Auriscalpium villipes*, plant pathogens like *Passalora* sp. and *Ophiostoma breviusculum* being ubiquitous taxa [37]. In another 7-yr observation in Spain, several core bacterial taxa were reported, e.g., *Sphingomonas*, *Methylobacterium*, *Massilia*, *Pseudomonas*, *Polaromonas*, and *Acidiphilium* among others [38].

While on seasonal scales, different patterns have been observed for the bioaerosol diversity. A clear seasonality has been detected for bacterial, archaeal, and fungal aerosols in the 7-yr observation in Spain [38]. Specifically, these microbial patterns were found to be strongly correlated with the air circulation regime related to season. However, no clear seasonality was observed in the tropic air of Singapore [33]. Specifically, microbial diversity in the tropical air exhibited more pronounced inter-day variations, which was mostly driven by the inter-day temperature variations.

On a daily scale, a clear diurnal pattern has been observed for the bioaerosol abundance, with a low level in the daytime and a high level in the nighttime as found in a previous study [4]. A significant diurnal change of fungal spores has also been reported in forested regions [39]. Similarly, a diurnal trend of the bioaerosol abundance was also observed in the tropic air in Singapore [33]. On the contrary, the diversity of bioaerosols in the tropical air followed an opposite diel cycle [33]. Specifically, the number of observed species of

Table 1 Concentrations and taxonomy of airborne bacteria, fungi and pollen in cities distributed in different continents[a]

	Continent	City	Concentration	Taxonomy composition (phylum)
Bacteria	Asia [9]	Beijing	10^2–10^5copies/m^3	Proteobacteria, Firmicutes, Actinobacteria, Cyanobacteria, Bacteroidetes
	Asia [16]	Beijing	10^5–10^6cells/m^3	Proteobacteria, Firmicutes, Actinobacteria, Bacteroidetes, Cyanobacteria
	Asia [17]	Ji'nan	$6.8×10^5±1.3×10^4$cells/m^3	Firmicutes, Proteobacteria, Bacteroidetes
	Asia [18]	Harbin	$6.0×10^1$–$3.4×10^5$copies/m^3	Proteobacteria, Firmicutes, Bacteroidetes, Planctomycetes, Epsilonbacteraeota
	Asia [9]	PRD	10^3–10^4copies/m^3	Proteobacteria, Firmicutes, Actinobacteria, Cyanobacteria, Bacteroidetes
	Asia [19]	Weihai	10^4–10^5cells/m^3	Proteobacteria, Firmicutes, Actinobacteria, Bacteroidetes, Deinococcus-Thermus
	Asia [20]	Xi'an	10^4–10^5cells/m^3	Proteobacteria, Firmicutes, Deinococcus-Thermus, Bacteroidetes
	Asia [9]	YRD	10^2–10^4copies/m^3	Proteobacteria, Firmicutes, Actinobacteria, Cyanobacteria, Bacteroidetes
	Asia [21]	Seoul	10^3–10^8copies/m^3	Firmicutes, Gammaproteobacteria, Deltaproteobacteria, Betaproteobacteria, Bacteroidetes
	Europe [10]	Puy de Dôme	$2.2×10^5$–$6.2×10^6$copies/m^3	Firmicutes, Bacteroidetes, Proteobacteria, Actinobacteriota
	Europe [22]	Pic-du-Midi	$1.5×10^5±1.3×10^5$copies/m^3	Proteobacteria, Firmicutes, Actinobacteria, Bacteroidetes
	North America [22]	Colorado	$1.6×10^6±1.2×10^6$copies/m^3	Firmicutes, Proteobacteria, Bacteroidota, Actinobacteriota
	North America [23]	Nuuk	10^1–10^3cells/m^3	Alphaproteobacteria, Rubrobacteridae, Acidobacteria, Firmicutes, Actinobacteriota
	South America [22]	Chacaltaya	$1.6×10^5±1.4×10^5$copies/m^3	Bacteroidetes, Firmicutes, Actinobacteriota, Chloroflexi, Proteobacteria
	Africa [3]	Bamako	$5.9×10^4$–$5.3×10^5$copies/m^3	Proteobacteria, Firmicutes, Actinobacteria
	Antarctica [24]	Antarctic coast	—	Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes
Fungi	Asia [13]	Beijing	10^3–10^4copies/m^3	Ascomycota, Basidiomycota
	Asia [25]	Ji'nan	10^2–10^4copies/m^3	Ascomycota, Basidiomycota, Zygomycota
	Asia [18]	Harbin	$1.6×10^2$–$7.9×10^3$copies/m^3	Ascomycota, Basidiomycota, Nematoda, Vertebrata
	Europe [10]	Puy de Dôme	$7.4×10^2$–$2.8×10^4$copies/m^3	Ascomycota, Basidiomycota
	North America [22]	Colorado	$8.8×10^4±6.5×10^4$copies/m^3	Basidiomycota, Ascomycota
	South America [22]	Chacaltaya	$1.1×10^3±1.0× 10^3$copies/m^3	Ascomycota, Basidiomycota
	Africa [22]	Cape Town	$1.7×10^2±1.2×10^2$copies/m^3	Ascomycota, Basidiomycota
Pollen	Asia [26]	Tokyo	$326±324$–$813±529$ pollen/m^3	Poaceae, Plantaginaceae, Araceae, mosses: Hylocomiaceae, Funariaceae
	Europe [27]	Cordoba	Peak: ($1287±898$ pollen/m^3)	Quercus pollen
	Europe [28]	Munich	0–1800 pollen/m^3(10^1–10^3)	Betula, Carpinus, Urticaceae, Poacea,Tilia
	Europe [29]	Vinmytsia	$8×10^3$–$3 ×10^4$pollen grains/m^3	Betula, Alnus, Fraxinus, Juglans, Acer
	North America [30]	Iowa	0–1100 pollen/m^3	—
	Africa [31]	Mornag	0–1400, 0–1900, 0–270, 0–80 pollen/m^3	Olea europaea , Cupressus, Urticaceae, Poaceae
	Oceania [32]	Queensland	789–3945 pollen/m^3	Poaceae, Fabaceae, Asteraceae, Myrtaceae, Cupressaceae

a) YRD: Yangtze River Delta region; PRD: Pearl River Delta region; "—" indicates data not available. Only data obtained with microscopy or PCR (unit: cells/m^3, pollen/m^3, copies/m^3) were provided here.

bacterial and fungal aerosols peaked at noon time (13:00) in a taxa-dependent manner. Of them, fungal phylum Ascomycota exhibited a higher daytime diversity peak and lower nighttime peak, while phylum Basidiomycota was relatively stable.

Spatial variations of bioaerosol abundance and diversity

Spatially, varying communities of bioaerosols have been observed on different scales. For example, significant variations at the global scale have been detected in a work which analyzed the bacteria and fungi in the outdoor settled dust collected from 33 countries and 6 continents [40]. Specifically, more than 90% of the bacterial and fungal taxa only appeared in less than half of the collected global samples, which was attributed to the stochastic processes in forming the airborne microbial community [40]. In this global study, annual precipitation and temperature were suggested to be the main environmental parameters that drive the microbial community composition variations. This prominent role of stochastic processes has also been revealed in another global scale study which covered 63 sites around the world [12].

On the regional scale, the impact of urbanization on the bioaerosols has been revealed by investigating and comparing the bioaerosol diversity between urbanized and less urbanized rural areas [4,12,41,42]. Our study in an urban site and a rural site in the North China Plain found that the urban site had higher levels of bioaerosols than those of the rural area and their bacterial community structures also differed significantly [4]. Another study also reported the contributions of human cooking activities to the ambient bioaerosols [43]. Some bacterial genera from human, including *Myroides*, *Streptococcus*, *Propionibacterium*, *Dietzia*, and *Helcococcus* among others, were higher in the urban site [4]. Within urban sites, green space was found to significantly affect the airborne bacteria and fungi, and could also reduce the level of pathogens [42]. Similar distinctions have also been reported when comparing the urban-rural sites and urban-suburban sites [41,44].

Vertically, distinct bioaerosol patterns were reported not only within the lower troposphere, but also up to stratosphere as high as 38 km [45,46]. The bioaerosol concentrations were found to be highest within the planetary layer (~10^6 cells/m^3), followed by the middle altitudes (~10^5 cells/m^3), and the stratosphere (10^4 cells/m^3). Bacterial aerosols collected at high altitudes included *Paenibacillus barengoltzii*, betaproteo-bacterial isolate L7-7A and actinobacterial isolates L6-1 and L9-4, which featured strong tolerance to desiccation and radiation [46]. Some taxa from families *Lachnospiraceae*, *Ruminococcaceae* and *Erysipelotrichaceae*, and genera (e.g., *Clostridium*, *Mogibacterium*, *Corynebacterium*, *Bacteroides*, *Prevotella*, *Pseudomonas* and *Parabacteroides*) were found to be more enriched in the high-altitude air [47]. Moreover, the aforementioned diel cycle was found to disappear at altitudes of more than 1000 m [45]. In addition to high altitudes, stratification of culturable bioaerosols has been found in an urban park even within a height range of 2 m above the ground, with the community structures immediately above the ground similar to those in the ground soil source [48].

Overall, the observed temporal and spatial differences in microbial levels and diversities are largely attributed to geospatial characteristics including climate, latitude, land use and human activities. The increasing trend of bioaerosol concentrations over such long-term period was correlated with the overall climate change context, while their relatively stable diversity in the recent decades was likely attributed to the underlying driving forces, e.g., stochastic process [37]. Both stochastic and deterministic processes collec-

tively determined the microbial community structures [49], while stochastic processes likely dominated in shaping the bioaerosol diversity in most normal circumstances and the latter may be more prominent in extreme environments [13,50,51]. Regarding more obvious seasonal variations, diel cycles and spatial distributions, atmosphere convection, and air circulation regimes were suggested to be important factors, which were mostly related to temperature gradients [33]. For instance, the nocturnal peak of fungal aerosol was associated with the wet-discharge of fungal spores in nighttime [33]. Moreover, anthropogenic factors (e.g., urbanization [52]) play a crucial role in the spatial differences on the horizontal direction.

Emission sources of rising concerns

Small biological entities are released from various natural and anthropogenic sources (e.g., soils, ocean, plants, animals and humans, and various man-made systems as shown in Figure 3). Depending on either external or internal forces, they were released in either active or passive manner [53]. Fungal spores were found to be released from the natural sources (e.g., soil, plant) in an active and finely tuned process, aiming to protect the spore viability [54]. This can be also exemplified by some filamentous fungi, which produce spores actively for reproduction. Specifically, ascospores and basidiospores were prone to be dislodged under wet conditions, like cooler nighttime and humid early morning [55]. Of course, there were some exceptions, *Alternaria* and *Cladosporium* spores were dislodged by external air forces under dry conditions. In addition, small sub-cellular components from the intact cell should not be ignored [30,56,57]. Although being released mostly from natural sources [58], climate change and urbanization has brought changes to the existing emission sources and the newly emerging sources. For instance, alarming concerns are rising from ocean, icy extreme environment and various human man-made systems [59,60].

Natural sources

(1) Sea spray

 Ocean covers 71% of the earth surface, and harbors roughly half of the bacteria and archaea existing on the
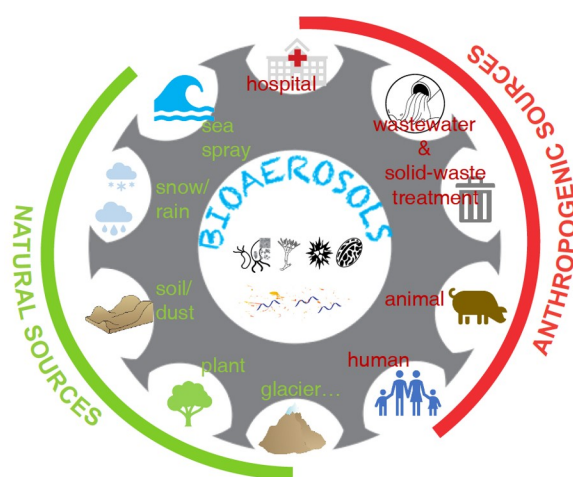
Figure 3 Natural and anthropogenetic emission sources of bioaerosols.

earth (5.5×10^{29} compared to the total $\sim 1 \times 10^{30}$ on earth) [11]. Large amounts of sea spray aerosols (SSAs) are produced through bursting bubbles, including jet drops and flapped film drops due to shear instability [61]. The roles of these SSAs in atmospheric chemistry and climate change have received profound investigations [62]. Thereby, SSAs of microbial sources have also received growing attention due to their chemical activity, IN activity and health effects [63].

Field observation and laboratory results added to the evidence regarding the contribution of seawater to bioaerosols. Release of bacteria and phytoplankton into the air via sea spray has been reported based on the fluorescence monitoring results from a pristine Antarctic ocean [64]. Another study also demonstrated the role of seawater in releasing bioaerosols by measuring and comparing the fluorescent spectra of laboratory generated SSAs and the bulk seawater [65]. Combining the chlorophyll a, transparent exopolymer particles (TEPs) and bacteria in the ocean, bioaerosols over the central Pacific Ocean were found to be predictable from the developed equations [66]. This means that changes in biological activities in the ocean could be directly linked to the changes in bioaerosol compositions.

Using fluorescence-based measurement technique, concentrations of bioaerosols above the pristine ocean were found between 370 to 1950 cells/m^3 and were slightly higher over the terrestrially influenced ocean area (580–2900 /m^3), accounting for 0.13% of the total aerosols (>1 μm) on average [64]. Bacterial aerosols collected over the Bohai Sea, the Yellow Sea, and northwestern Pacific Ocean were dominated by phyla Bacteroidetes (26.99%), *Firmicutes* (26.72%) and *Proteobacteria* (21.82%), while the distribution of bacterial genus (e.g., *Bacteroides*, *Prevotella*, *Megamonas*, *Paracoccus*, *Sphingomonas*, *Pseudomonas*) varied across the sampling sites [67]. Fungal aerosols over the Northern South China Sea were dominated by phylum Ascomycota and Basidiomycota, however, the Ascomycota/Basidiomycota ratio over the sea was lower than those continental fungal aerosols [68].

The aerosolization process of oceanic biologicals was suggested to be selective in a type-dependent manner [69]. Hydrophobic properties and capsules were reported to be able to facilitate the aerosolization process [69]. Specifically, several microbials (e.g., taxa from mycolic acid-coated Corynebacteriales, and virus with lipid-envelope) were easier to be aerosolized, while some taxa (e.g., *Flavobacteriia*, some *Alphaproteobacteria*, and *Caudovirales*) were less capable to be aerosolized. Several taxa with capsules (e.g., *Bacillus*, *Pseudomonadales*) were also found to be easily aerosolized.

In addition to the surface microorganisms, even those in the deep ocean could also be transported to the surface and then into the air. This has been observed in the summertime phytoplankton bloom in Arctic Ocean area, where sea ice was experiencing rapid diminishment [70]. The direct consequence of this process was the provision of massive microbial INs into the Arctic atmosphere, which could affect the cloud and then the precipitation and climate.

With the frequent occurrence of harmful algae blooms, toxins aerosolized from the marine systems have also raised a serious health concern [71]. For instance, phycotoxins from marine harmful algal blooms have been observed in the SSAs with an enrichment up to 1769-fold compared to the surface water [72]. In addition, harmful algal blooms in the freshwater system also could release related toxins into the air, e.g., cyanotoxins from cyanobacteria [73–75].

In the context of climate change, ocean would face a warmer temperature, more stratified layer and more carbon dioxide. These factors might largely affect the oceanic phytoplankton and sediment biomass. As a biological link between the ecosystem of ocean, atmosphere and others, it is necessary to further explore the

effects of ocean-derived bioaerosols on coastal climate and health. The taxonomy, pathogenicity, and toxicity of bioaerosols from sea spray should be continuously monitored. Considering the strong IN activity of certain bioaerosols, the amount and capacity of bioaerosols over ocean with IN activity should be comprehensively investigated and parameterized into the climate model.

(2) Atmospheric events

Sand and dust storms occur frequently and present great concerns due to the high percentage of desert and semi-desert areas (40% of the land surface globally). This sand dust could transport up to thousands of kilometers. Along with high levels of coarse particles, abundant and diversified microorganisms are found within the dust particles [76]. According to metagenomic results, bacterial taxa were found to dominate the dust microbiome, followed by fungi, archaea and virus [77,78]. Notably, genes related to UV-induced DNA damage repair and aerosolization were ubiquitous in these dust-borne microorganisms [77]. Potential pathogens like virulent genus *Bacillus cereus*, have been isolated from dust samples [21]. However, dust was not assumed to be a transport vector for ARGs as indicated in one study [79].

Outbreak of sand storm transports significant exogenous microorganisms from the dust source [80]. Accordingly, transient changes of abundance and community structure have been widely observed [81,82]. This was in particular apparent at the high-altitude free troposphere (>1200 m), where the bioaerosols increased one to two orders of magnitude during the dust events (roughly from 10^4 to 10^6 /m^3) [83]. Besides the increase of absolute level of bioaerosols, the fraction of bioaerosols in the total aerosols also increased from a mean level of 0.4% to above 1% during dust events, which was likely due to the abundant microorganisms in the arid soils [84].

Except the abundance increase, significant changes of community compositions started early from the ground air of dust origins and continued along the transmission route [83]. With the onset of sandstorm, the vertical distribution patterns of microbial community varied in a type-dependent manner, with the bacterial community mixing more evenly and fungal community showing more varieties [85]. Along the transport pathway, distinct bacterial structures have been reported in different sites during the outbreak of one dust event [86]. When comparing the microbial and chemical components in the dust, the occurrences of ammonia oxidizing archaea, high levels of viable, cultivable and metabolically active microorganisms were likely accompanied by the high nitrate concentration and high trehalose levels [51,86–88]. Based on this, there is a possibility that dust-borne microorganisms could actively participate in the nitrogen biogeochemical cycling.

In addition to sand dust storms, the frequency of extreme precipitation events also increases recently. Due to the high efficiency of bioaerosols in cloud formation, it is of great importance to clarify the role of precipitation in redistributing bioaerosols. Along with the precipitation, bioaerosols transmitted over long distances and those suspended in the atmosphere could deposit into the local environment via with-cloud or below-cloud scavenging mechanism [82,89]. Apart from bringing exogenous bioaerosols (e.g., ARGs, pollens) [90–92], rain events were also found to lead to the additional release of bioaerosols. Various factors accounted for the rain-induced increase, including the microorganisms from the rain drops, the resuspension from soil/leaf surface, the wet splash droplets and the air vortex [93,94]. Significant increases of fungal spores, bacteria (especially autotrophic bacteria like cyanobacteria) and endotoxins have been reported [92,95]. Moreover, the ruptured pollen during the rain also released lots of small particles in the fine size range [30,96,97]. Likewise, fungi released nanoparticles into the air episodically [57]. These newly released bioaerosols were found to be able to impact cloud formation and the precipitation feedback in a few days or

several weeks [98].

In addition, melting and retreating of glacier and frozen soil due to climate change could also bring more microorganisms into the air. Dust released during the retreat of glaciers contributed large amounts of biological INs [99]. Different atmospheric circulations were found to be able to blow various bacterial taxa to the air above the glacier over the Tibetan plateau [60].

Due to the role of atmosphere in connecting various ecosystems, the atmospheric events certainly play a role in redistributing the microbials across the ecosystems. Considering the significant impacts from desertification, increased precipitation and drought, glacier melting and thaw of frozen soil on the earth system, microbials stocked within these ecosystems could possibly be released and spread via airborne route, resulting in increased risks for both human and ecosystems. Therefore, it is necessary to further elucidate the dynamics of biological characteristics during the atmosphere processes and also the effects of their deposition on the earth surface ecosystems.

(3) Natural soil and plant emission

As a highly diversified ecosystem, soil is rich in various microorganisms [100]. The release of soil microorganisms into the air has been well exemplified by the bioaerosol vertical distribution above the soil surface [48]. In this study, the results showed that microbials within the height of 0.5 m shared more community similarities compared to those within the height of 1.0–2.0 m. By using low-molecular-weight beta-hydroxy fatty acids as indicators, soil-derived microbials were suggested [101]. Fertilization of the soil with manure was found to be able to increase the soil bioaerosol emission, which decreased after the integration of manure into the soil [102]. Besides, microorganisms from the biological soil crusts also dispersed widely [103]. Raindrops falling onto the soil could induce the dispersal of soil-microorganisms [94]. According to wind tunnel studies, the aerosolization of microorganisms from soils was associated with the microbial types [104].

As a habitat for microorganisms, plant surface (phyllosphere) is a large microbial pool [105]. The urban airborne bacteria and fungi were found to be affected by the areas of urban green area and the plant species [42]. Leaf-enriched bacteria, e.g., *Massilia*, *Pseudomonas*, *Frigoribacterium*, and *Sphingomonas* were positively associated with the airborne sugar compounds, indicating the role of plants in shaping the airborne microbiome [106]. Both plant probiotics and pathogens have been observed in the atmosphere [107,108]. Using high-speed photography, liberation of rust fungus *Puccinia triticina* was observed upon the fall of raindrops on the surface of infected wheat plant [93]. Another study in vineyards also reported the contribution of grape plantings to the airborne fungi [109]. Catkins from plants were also found to be bioaerosol carriers [110]. Moreover, one study using rRNA amplicon sequencing showed that more than 40% of the plant-derived fungi in the air were active [111].

Soil and plants provide natural and healthy environment and food to humans, which are partly inter-mediated by the microorganisms. However, increased agricultural activities, urbanization, and climate change are exerting increasingly high pressures on these two ecosystems. The global areas of land surface and leaf surface are estimated to be 1.5×10^8 and 6.4×10^8 km^2, respectively; and the microorganisms on these surfaces generally ranged between 10^4 and 10^8 cells/cm^2 [112]. The emission fluxes of bacteria and fungal spores were in the order of 10^2 m^{-2} s^{-1}, demonstrating a high-throughput exchange of microorganisms between the air and the land or leaf surfaces [2]. Therefore, the response of the soil and plant microbiome to the external forces could immediately affect the bioaerosol flux from them. Thereby, microbial structure

change, pathogenicity, and even ARGs of the bioaerosols released from the soil or plant microbiome should be explored.

Anthropogenic sources

(1) Emission from man-made systems

Due to rapid increase in population density in various areas, especially the urban cities, requirements on the treatment of the wastewater and solid waste from citizens have resulted in the construction of a large number of wastewater treatment plants (WWTP) and solid waste management systems. WWTP treatment units with aeration, mechanical agitation, and sludge were supposed to be the main emission sources, and the levels of the corresponding airborne viable microorganisms close to the aeration tank ranged from 5×10^4 to $1.4 \times 10^5/m^3$ [113]. Likewise, solid waste treatment system also contributed significantly to the airborne bioaerosols, which mostly came from the leachate and solid waste [114,115]. Moreover, although resource recycling prompted the development of circular economy, several practices, e.g., waste recycling and water reuse, have brought new concerns. Specifically, bioaerosol release has been reported from various processes, including waste collection, sorting, storage and pretreatment processes [116]. Of them, enteric bacteria/virus, specific pathogens (e.g., *Legionella*, noroviruses, human adenovirus (hAdV), drug-resistant, *Staphylococcus*, *Aspergillus* spp.), toxins metabolized by the microbials (e.g., endotoxins, mycotoxins), and also ARGs, pose significant health risks to the nearby exposed people [116–123]. Interestingly, one study showed that the aerosolization capacity of microbes depended on their types [124].

Aiming to keep human healthy, hospitals in turn have become a hotspot for the accumulation and spread of various pathogens and ARGs [125,126]. The ARGs in the hospital air were found to be nearly twice as those in the urban air [126]. On one hand, patients who carry pathogens and ARGs contribute to the airborne bioaerosols [127]. On the other hand, several clinical practices especially those in the dental department could result in bioaerosol release. In addition, the spreading risk from the HVAC (heating, ventilation, air conditioning) system and toilet flushing should also be taken seriously [128,129].

While these man-made structures are used to improve our living conditions, they also bring new risks. Microorganisms within these man-made systems are facing high mutation pressures, e.g., accumulation of chemically synthesized pollutants, medicines like antibiotics, which have greatly changed the exposome of microorganisms. Thus, microbial evolution in these systems is becoming a critically important topic and bioaerosol surveillance should be established to understand these processes.

(2) Human and animal sources

It is already a consensus that human co-lives with microorganisms. Therefore, microorganisms living within and on the human body could be released into the air via human breathing, talking, sneezing, coughing and skin peeling [130–133]. Humans were reported to release 2.1×10^6 viable microorganisms into the air per hour [131]. Microorganisms in the feces and urine could enter into the air via toilet flushing processes [134]. Besides, human activity, such as walking, also could induce the resuspension of bioaerosols from ground dust [135]. The contribution of human release matters particularly in indoor environments and other relatively closed spaces. Even in the open ambient environments, human-related bacteria have been revealed especially certain pathogens [12].

The current COVID-19 pandemic is a good example demonstrating the role of humans in releasing

bioaerosols. Millions of SARS-CoV-2 viruses were released from human exhaled breath per hour, indicating the role of exhaled virus in spreading the disease [136]. Meanwhile, SARS-CoV-2 viral aerosols were also detected at high concentrations in the toilets, implicating a risk from toilet flushing [136]. Among others, lack of effective measures in controlling the aerosol transmission route of SARS-CoV-2 has resulted in huge disruption from this COVID-19 pandemic to the society and loss of life. Meanwhile, emerging pathogens, e.g., Monkeypox virus, further add to the social panic during this COVID-19 pandemic [137].

In addition to human emission, contribution from animals also cannot be ignored. Bioaerosol emissions from large-scale farming of livestock have been widely reported [138,139]. Livestock-related bacterial genera *Staphylococcus* spp. in the air within a radius of 1 km of a farm reached 3.7×10^4 gene copies/m^3 [139]. Notably, the wide usage of antibiotic in breeding has enhanced the risk of ARGs spreading [140]. From the one health perspective, the health of humans, animals, plants and environment on the global scale are closely interconnected via microbiome [141]. Therefore, antibiotic-resistant microbials and ARGs emission and spread from the livestock should be closely monitored and predicted [142]. This article mainly focused on the earth system (health, ecology and climate), and detailed discussion of airborne transmission of infectious diseases can be found elsewhere [143–146].

Interaction between bioaerosols and air quality

Recognizing that microorganisms could not only be transported through the air but also keep their survival, it is important to clarify whether the atmosphere is just a transport route [46,147,148] or can be a living sphere for microbes. However, current knowledge on the role of bioaerosols in air quality and climate change is rather limited.

Dynamics of bioaerosols under conditions of haze pollution

Air pollution featuring hazy weather has promoted a large number of studies on the formation and impact of haze episodes in the Northern China Plain [149,150]. Meanwhile, dynamics of bioaerosol characteristics which evolve over time have been widely studied, including their concentrations, size distribution, diurnal variation, and community structure in several cities of China. Table 2 summarizes most of the studies which investigated the bioaerosols under haze days in China published since 2016. From this table, it could be seen that various indicators were used in the previous literature. These varying indicators included the total primary biological PM, viable biological PM, total bacterial PM, total fungal PM, total archaeal PM, culturable bacteria, culturable fungi, and endotoxins depending on the analysis methods.

Different bioaerosol abundance trends under hazy weather have been reported. Using traditional culture-based method, increases of culturable bacteria and culturable fungi were widely reported during haze episodes in different cities of China, including Beijing, Xi'an, Qingdao, Jinan [157], and even mountainous areas[161]. However, distinct trends were observed when the other culture-independent indicators were applied [152,153,159,164]. Furthermore, an increase at the initial stage of air pollution and a decrease or plateau at the later stages have also been reported when the haze episodes were finely classified into different levels [4,16,51,152,154]. Moreover, a study performed in Xi'an found that this increase was found at low

Table 2 Publications (2016–2022) that investigated the bioaerosols under haze air pollution in China[a]

Sampling period	Type [refs]	Sampling time; duration	Sampler type; flow rate	Size range	Sampling height	Location	Abundance analysis	HTS
2013.01–2013.02	Bacteria, Fungi [151]	—; 8 h/ (haze); 12 h/ (non-haze)	Biosampler; 12.5 lpm	—	22 m	Beijing	—	√
2013.01–2014.01	Culturable bacteria & fungi [152]	8:00, 13:00; 10 min/sample	Anderson six-stage sampler; 28.3 lpm	Size-resolved	20 m	Beijing	Culture	—
2013.06–2014.06	Viable microbes [4]	Real-time	UV-APS	Size-resolved	20 m	Beijing, Wangdu	—	√
2013.10–2014.08	Total microbes [153]	8:00–8:30; 30 min/sample	Filter sampler; 28.3 lpm	Size-resolved	Roof top	Qingdao	DAPI staining	—
2013.12–2014.03	Viable microbes [154]	Real-time	UV-APS	Size-resolved	22 m	Beijing	—	√
2014.01–2014.03	Bacteria [155]	9:00–08:00 +1 d, 23 h/sample	Filter sampler; 30 lpm	PM_1	20 m	Jinan	qPCR	√
2014.07–2014.11	Fungi [156]	12:00–12:00 +1d, 24 h/sample	Filter sampler; 5 lpm	$PM_{2.5}$ PM_{10} TSP	Roof top	Beijing	—	√
2014.08–2015.07	Culture bacteria & fungi [157]	—; 20 min/sample	Anderson six-stage sampler; 28.3 lpm	Size-resolved	40 m	Xi'an	Culture	—
2015.10–2016.01	Bacteria [16]	—; 1–2 h/sample	Filter sampler; 16 lpm	Total	22 m	Beijing	Live/dead viability kit staining	√
2016.04–2016.05	Bacteria [158]	9:00–9:00 +1 d; 24 h/sample	Filter sampler; 100 lpm	$PM_{2.5}$ PM_{10}	22 m	Beijing	—	√
2016.04–2017.02	Bacteria [159]	—; 50 min/sample	Filter sampler; 5 lpm;	Total	20 m	Xi'an	DAPI staining	√
2016.10–2017.01	Bacteria [160]	—; 75 min/sample	Filter sampler; 16.7 lpm	$PM_{2.5}$ PM_{10} TSP	1.5 m above roof top /above ground	Xi'an	DAPI staining	√
2017.01	Culturable bacteria, total bacteria [161]	Every 2 h; 10 min /sample	Anderson six-stage sampler; 28.3 lpm	Size-resolved	15 m	Xi'an	Culture	√
2017.08–2017.12	Total bacteria [17]	8:00; 10 min/sample	Liquid sampler; 10 lpm	—	1 m	Jinan	Flow cytometry	—
2017.08–2018.04	Fungi [162]	24 h/sample	Filter sampler; 1 m³/min	$PM_{2.5}$ PM_{10}	Roof top	Harbin	—	√
2017.09–2018.01	Pathogenic bacteria [163]	24 h/sample	Filter sampler; 16.7 lpm	$PM_{2.5}$ PM_{10}	Roof top	Xi'an	—	√
2018.01	Fungi [164]	9:00–17:30, 8 h; 17:45–8:45 +1 d, 15 h/sample	Filter sampler; 1 m³/min	$PM_{2.5}$	15 m	Wuhan	—	√
2018.03	Archaea [51]	—; 3 h/sample	Biosampler; 12.5 lpm	—	29 m	Beijing	qPCR	√
2019.09–2020.01	Total microbes [20]	—; 1–2 h/sample	Filter sampler; 16.7 lpm	$PM_{2.5}$	20 m	Xi'an	DAPI staining	√
2019.12	Bacteria, fungi, archaea [165]	Every 4 h	Filter sampler; 100 lpm	$PM_{2.5}$	4 m	Xi'an	—	√

a) "—" indicates data not available; HTS: high throughput sequencing; "√" indicates that this study applied the HTS technique.

height levels (1.5 m, 100 m) but not at the height of 229.5 m [20]. The haze stages- and height-dependent changes suggest a possibility of the haze pollutants on the bioaerosol abundance.

In addition to the abundance, taxonomic structures of bioaerosols were also affected [151,156,158,165]. A type-dependent variation has been found for bacteria, fungi and archaea during a haze process. Specifically, bacterial composition changed substantially at the onset of haze pollution, and kept steady during the haze period; while composition of ammonia oxidizing archaea and fungi varied all the time [20,164]. Moreover, this change trend was more about a decline in the microbial species richness, indicating a potential selection pressure on the airborne microbes. It is worth noting that a significant variation was observed for bacterial taxa within submicron particles [155], suggesting a possibility of microbial metabolic reproduction process. However, inconsistent results were also reported elsewhere with no significant structure change [13,160].

Overall, despite some inconsistencies, the impact of hazy air on the abundance and diversity of bioaerosols is clear, which depends on both haze conditions and microbial types. And this impact on bioaerosols would be directly linked to certain adverse health effects. For instance, the increase of certain pathogens, opportunistic pathogens, especially those belonging to the fine particles (<2.5 μm) that could enter into the lung, raised severe health concerns [156,162,163]. Meanwhile, ARGs carried by some microorganisms (e.g., NDM-1 and vanB carried by *Bacillus halotolerans*) have also raised further alarms due to their sharp increase in severely polluted air [166]. On the other hand, bioaerosol dynamics in the haze air also indicate a possibility of bioaerosol involvement in the atmospheric chemistry, which will be discussed in the next section.

Up to now, most of the studies on the bioaerosol dynamics under hazy weather were observational. Less is known regarding the driving forces underlying the bioaerosol dynamics related to hazy weather. Considering the complexity of haze development, further in-depth study should be performed to elucidate the bioaerosol dynamics from a microscale and even a molecular level. Moreover, a comprehensive understanding on the interaction between bioaerosols and air pollutants is much needed. Laboratory hypothetical and model investigations could make up the shortcomings of these field observational studies.

Role of bioaerosols in air pollution

Current understanding on the formation of air pollutants

Hazy weather happens frequently in China and several other countries, featuring rapid increase of PM and persistent high PM levels. These PMs harbor high levels of sulfates, nitrates and secondary organic aerosols (SOA). Su *et al.* [167] reviewed the current understanding on the formation processes of these pollutants, mainly by the gas phase photochemical reactions and multiphase chemistry. Specifically, high concentrations of sulphate could be explained by the multiphase reactions between SO_2 and NO_2 within aerosol water at pH>4.5, while between SO_2 and transition metals and H_2O_2 at pH<4.5. For the nitrates, one pathway involves the gas phase oxidation of NO_2 by OH radicals, and the second pathway involves the aqueous phase hydrolysis of N_2O_5 produced from the gas phase NO_2–O_3 reaction; and the latter N_2O_5 pathway is favored at the conditions with high PM concentration and high humidity. For the SOA, two pathways are involved. One pathway is the gas phase oxidation of VOCs (volatile organic compounds) and further partition onto the particle phase; and the second one is the direct reaction of VOCs/SVOCs (semiVOCs) within the aerosols, clouds and so on. Therefore, heavy hazy weather still happened alongside the reduced primary pollutant

emission, which was mostly related to the formation of secondary pollutants [168]. In addition to haze pollution, increase of O_3 appeared along with the gradual decrease of PM levels [169,170].

Potential role of bioaerosols in air pollution

As a complex mixture of various inorganic and organic compositions, bioaerosol could possibly play a role in the atmospheric multiphase chemical processes (Figure 4), which is currently largely ignored.

Firstly, large amounts of viable cells were found in the bioaerosols. As shown above, the increase of culturable and viable bioaerosols has been widely observed during the haze days. Zhang *et al.* [171] detected a high fraction of viable cells during the severe haze air pollution along with increases of other inorganic ions (SO_4^{2-}, NO_3^- and NH_4^+). In addition, significant changes to the microbial aerosol structures have been observed. It is certain that microbial growth was involved in the aerosol chemistry. However they did not provide an estimate for the bioaerosol production rate, due to the fact that it was a complex real environment featuring many different pollutants at one time. Besides haze pollutants, more than half of the attached bacteria on the long-range transported dust was found viable during the sand dust events [7]. According to a previous literature, aqueous-phase sulphate production at neutral pH range of 7–8 was two to three orders higher than those at the pH range of cloud droplet (pH 3–5) and of Beijing haze particles (pH 5.4–6.2). Based on the general pH range of microorganisms (7.5–7.7) [172], there is a possibility of faster sulfur dioxide oxidation rate within the microbial cells. Besides, free metals like manganese within bacterial cells were suggested to be in the range of 10^{-6} to 10^{-5} mol L^{-1} [173], which is comparable to those in the cloud droplets [149]. However, few experimental data are available regarding the uptake coefficient and reaction kinetic parameters within or on the surface of microbial cells, which is a challenge to be addressed in future studies.

Secondly, bioaerosol metabolism has been revealed using various analysis methods. Generally, micro-organisms suspended in the air were supposed to be in a passive state due to the harsh atmospheric conditions. By applying comparative 16S (18S) rRNA/rDNA ratios, highly metabolic bacterial and fungal aerosols have been reported in the field studies [87,174]. Functional prediction based on the amplicon sequencing
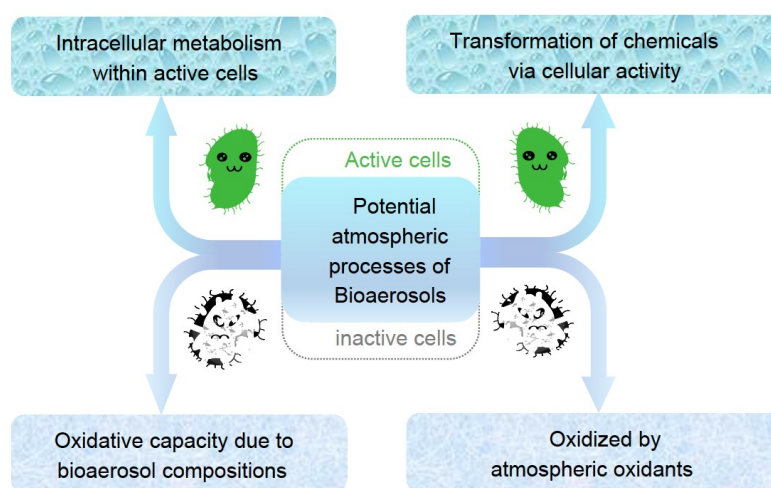
Figure 4 Potential reaction pathways of bioaerosols in the atmosphere.

results also revealed the potential enhancement of several signaling pathways, including metabolism of cysteine and methionine, biosynthesis of lysine, valine, leucine and isoleucine during the haze period [175]. Another functional study also suggested the possible interactions between $PM_{2.5}$ components and bacterial metabolism [111]. Moreover, laboratory experiments showed that bacterial aerosols could actively modulate their gene expression including the general stress gene (rpoS) and oxidative stress genes (oxyR, soxR) [176]. Using metagenomic data, high proportions of urban fungal aerosols were suggested to be associated with the high ratios of genes related to stress, including desiccation, UV and oxidative stress [177]. Meta-tran-scriptomic technique also revealed the metabolism of microorganisms in the cloud. Specifically, their transcriptional and translational activities were closely related to the cellular responses to oxidative stress, osmotic stress and cold environment [178]. Meanwhile, biodegradation of phenol and catechol by bacteria has been found to be comparable to the chemical degradation pathway in the cloud [179]. Hence, based on the observed associations and laboratory simulation experiments, the metabolic activity of viable bioaerosols could likely be involved in the formation of secondary air pollutants.

Thirdly, even without viability, the airborne microbial cells could possibly influence the atmospheric processes through releasing its intracellular components. Oxidative capacity of atmosphere is a key factor that drives the formation of air pollutants. Samake *et al.* [180] found that both viable microbial cells and inactivated cells exhibited similar oxidative potential, and could even enhance the oxidative potential of chemicals. Thereby, bioaerosols could affect the chemical processes in the air via their oxidative potential regardless of their metabolic activity.

Additionally, chemical interactions between bioaerosols and various chemical components have been revealed via heterogeneous and multiphase processes [181]. Laboratory study showed the immediate reaction between single fungal aerosol and ozone, especially between lipids and protein and ozone [182]. Besides, biologicals like endotoxins within the sea spray aerosol were found to be able to react heterogeneously with gaseous HNO_3, and this reaction was affected/modulated by the cations [183,184]. Even in urban air, nitrification of bovine serum albumin (BSA) protein sample was observed by the ozone and nitrogen oxides in the ambient air [185]. By comparing the proteinaceous components in the air before and during the 2014 Asia-Pacific Economic Cooperation summit, atmospheric oxidants (e.g., ozone, free radicals and nitrogen dioxide) were found to play a role in transforming the airborne proteins [186].

Accordingly, it is possible that bioaerosols could affect the atmospheric multiphase chemical processes and even play a role in the formation of secondary air pollutants (Figure 4). On one hand, they might be actively involved in the atmospheric chemical processes via their own metabolic processes. On the other hand, they might participate by contributing their intracellular biological macromolecules or trace elements.

## Linkage between bioaerosols and climate system

It is well appreciated that microorganisms have an important role in regulating climate change [187,188]. Bioaerosol could play an intermediate role via its cycle of emission, transport and deposition among the five components of the climate system, including the atmosphere, the biosphere, the hydrosphere, the cryosphere and the lithosphere [189]. However, role of bioaerosols in the climate change has not received comparable attention due to the fact that microorganisms in the atmosphere are orders of magnitude lower than those in

the ocean and soil [11]. As particles floating in the air, bioaerosols could affect climate change by scattering/ absorbing the solar radiation directly or affecting the cloud indirectly (Figure 5). Moreover, the chemical and biological processes of these viable bioaerosols could even drive the production of secondary components and their interactions with clouds in the atmosphere [190,191]. In addition, bioaerosols could also likely affect the fluxes of greenhouse gases (GHG) indirectly via affecting the GHG sources, for example, soil, permafrost, lake and ocean.

The particularity of bioaerosols is that some airborne biological components harbor ice nuclei protein (INP). These biological INPs are efficient IN at relatively warm temperatures at which mineral dust could not. The hydrogen bond and hydrophilic-hydrophobic patterns of the INPs could reorder the water molecule at the air-protein interface [192]. This means that bioaerosols likely play a critical role in the formation of mixed phase cloud at intermediated altitudes where the IN efficiency of mineral dust is low.

Not only the intact cells but also the macromolecules are efficient INP [193,194]. For example, fragments from pollen/fungi showed an increased water uptake above ~95% RH [195]. And these fragments with IN activity were mostly smaller than 0.45 μm [196]. Atmospheric aging processes, including radiation, acid-ification and oxidation, could affect the IN activity of these fragments [196]. This might partly explain the inconsistency regarding the role of bioaerosols in the ice crystal formation in previous studies. These studies explored differential subjects by applying different analysis approaches (e.g., online measurement with fluorescence-based instruments (UV-APS, WIBS) [197,198], laboratory offline analysis (biomarker mea-surement, microscopy staining, qPCR and high throughput sequencing) [199–201]). Considering the increase of pollen/fungal spores driven by the gradual increase of carbon dioxide, temperature and extreme events, it is necessary to determine the feedback between bioaerosols and the climate.

Transport of bioaerosols could impact the climate system by redistributing the efficient biological INPs. Long range transport of bioaerosols has been observed in various field campaigns, including those in Antarctica, high mountain and ocean surface, which could be as far as thousands of kilometers and at a transcontinental level [81,202–204]. According to the data from a Circumnavigation Expedition, around 33%–68% of the airborne microorganisms over the ocean originated from the ocean, while the remaining
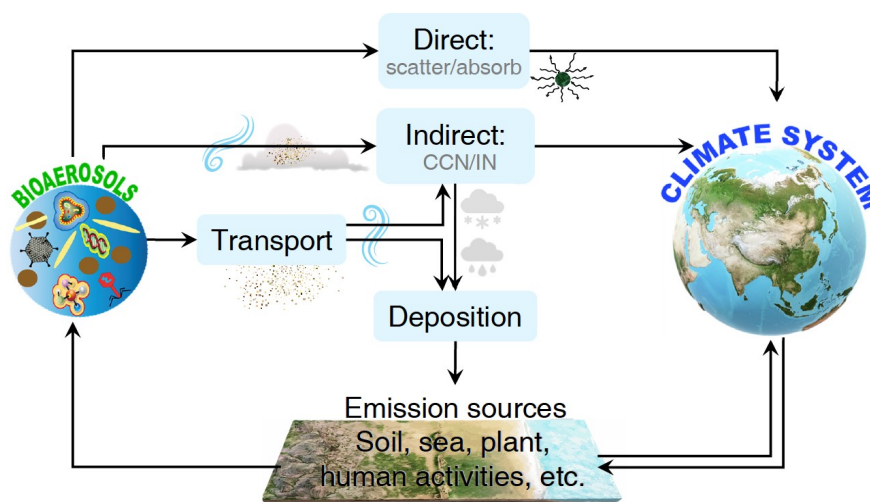
Figure 5 The impact pathways of bioaerosols on the climate system.

originated from the distant land/island [203]. Air masses passed through densely populated areas differed with those through natural areas [205]. Long range transport of Asia dust was suggested to provide microbial ice nuclei particles to Japan [206].

In addition to its spatial redistribution, bioaerosol deposition after long-range transport could directly affect the local ecosystem. In the polar ice core, a vertical deposition pattern of bacterial cells was clearly seen, which well illustrated the impact of transported bioaerosols in a time-series manner [207]. From the point of a fixed site, bioaerosol deposition not only brings along the possible nutrient input [208], but also leads to an invasive risk of alien species. Colonization of sterile soil by bioaerosols could happen within one day [209]. Several mesocosm experiments have been performed to identify this risk in the oligotrophic seas. In particular, deposition of sandstorm dust was found to exert disturbance on the bacterial abundance and diversity, bacterial production, dinitrogen fixation and the microbial structures [210–212]. In the oceanic area, deposition of dust particles also brought certain amount of microbials to the ocean surface water, with some exhibiting immediate microbial activity in the destination [213]. Except the open area like ocean, surface microbial ecosystem in the lake [214], the crop land [215], and the soil [216] could also be affected by the deposited bioaerosols. Subsequently, feedbacks from these affected underlying surface systems would affect the local climate even globally. In contrast, the impact of bioaerosol deposition on the phyllosphere microbiome seems to be limited [217].

The final impacts of deposited microorganisms also depend on the localized nutrient, environmental parameters as well as the habitat microorganisms [218], which could be related to the priority effects [219]. From these studies, it is clear that bioaerosol deposition definitely exerts certain effects on the local microbial ecosystem. Subsequently, they would affect the biogeochemistry and the climate. Therefore, exploration of the role of bioaerosol in shaping the global microbial biogeography is necessary. On long time scales, it is of prime importance to determine how the climate change impact/modulate this bioaerosols-local ecosystem-newly released bioaerosols/GHG network [70].

Overall, it is clear that bioaerosols of certain types are good INs, and are currently a research hotspot. Correspondingly, their deposition onto the earth surface could then impact humans and environment. Subsequently, the release of bioaerosols from the affected human and earth environment would be affected. Thereby a bioaerosol release-deposition loop between the atmosphere and earth system is formed. Disruption to this microbial balance could have far reaching consequences. Interactions between microbiota in the air, air quality, and air pollutants could directly affect this loop and finally affect the ecology, climate and human health.

Health effects of bioaerosol exposure

Our understanding on the health effects of bioaerosols starts from pathogens which can transmit through the air (Figure 6). With the discovery and large application of antibiotics, ARGs dissemination via air has also received growing attention [220]. Meanwhile, airborne allergens were found to be the main inducer for inhalable allergenic diseases [221,222]. Recently, the entire bioaerosol ensemble constitutes a part of human external microbiome and likely plays a role in both human health and disease from the point of immunology [223].
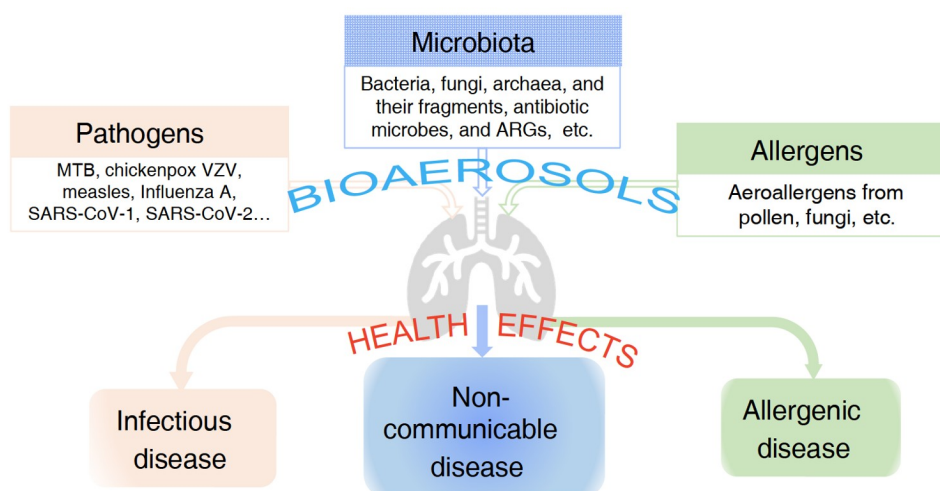
Figure 6   Illustration of health effects of bioaerosols.

Infectious disease transmission via airborne route

Aerosol transmission of certain pathogens

Arising from disturbance to ecosystem, the frequency of emerging infectious disease outbreaks is increasing. Up to now, pathogens that could not only induce disease but also spread between humans via air include *Mycobacterium tuberculosis* (MTB) [224], varicella-zoster virus (VZV) for chickenpox, measles virus, Influenza A [225], parainfluenza virus, respiratory syncytial virus, human adenovirus, human coronavirus, human metapneumovirus, SARS-CoV-1 and SARS-CoV-2 [226]. Before the COVID-19, only precautions against the VZV and measles transmission are recommended in hospitals [226]. The reason behind the airborne transmission of a pathogen lies in the fact that the pathogens can induce disease via inhalation route. Before being inhaled, they need to be able to sustain their viability. Meanwhile, they need to be released in large amounts, and substantial viable cells are inhaled by the recipients to launch an infection. Therefore, several factors should be considered, including the amount of released pathogens, the viability of transmitted pathogens, environmental parameters (e.g., temperature, humidity, solar radiation), the matrix or co-existing particles, the size distribution, and also the susceptibility of the exposed subjects [226].

Typically, atmospheric parameters (e.g., humidity, temperature and pollutants) could affect the viability of pathogens, thus on their airborne transmission ability [227,228]. Efflorescence and deliquescence were suggested to account for the effects of humidity on the survival of aerosolized viruses [229,230]. Additionally, the compositions of the lung fluid also significantly affected the survival of exhaled pathogens, which even could offset the effect of humidity [231]. Certain active cells (e.g., *Escherichia coli*, *Klebsiella pneumoniae*) could actively modulate their gene expression in response to the change of humidity and temperature [232].

Aerosol transmission route plays a crucial role in the outbreak of many pandemics in the history [143,144]. During the COVID-19, there are numerous studies regarding the airborne transmission of pathogens. Some reviews can be referred to [145,146,233]. However, even for the COVID-19, it still took almost two years for the WHO to admit the importance of aerosol transmission route [234]. In addition to the influence of

subjective wishes, it was also objectively related to the lack of valid evidence. Fortunately, several important evidences came out during the COVID-19 pandemic, for instance, detection of SARS-CoV-2 in the exhaled breath condensate of COVID-19 patients [136], viral DNA in the aerosol samples [235], direct detection of viable virus in the air more than 2 m away from the COVID-19 patients in the hospital room, epidemiological evidences regarding the outbreaks in a special hand-shake building [236], in buses [237], among singers of Skagit Valley Chorale [238], in care hospitals [239], and on the Diamond Princess cruise ship [240]. All these serve as solid evidences on the aerosol transmissions route [241]. However, it should be mentioned here that the aerosol transmission route of SARS-CoV-2 does not exclude the role of direct transfer by large droplets (>100 μm) [242]. These large droplets behave differently to the aerosol particles. They directly fall on the mucous membrane of the exposed person, and play an important role in direct infection within short distances (<2 m).

Reaching such a consensus, novel research pattern and techniques are needed to be established by scientists from multidisciplinary fields, including the aerosol science, microbiology, immunology, epidemiology, and architecture. The viability dynamics and their influencing factors need further in-depth investigation.

For the known pathogens, detection in their original status with high sensitivity, rapid identification and screening of the emission sources, are especially important. Thereby, improved sampling methods with low damage and high enrichment, and quantification methods with fast speed and high sensitivity are crucial.

While for the unknown potential pathogens, continuous surveillance is crucial to detect the potential harm timely. Humans face increasing exposure to unknown pathogens, for instance, bats-carried viruses are projected to be encountered with higher frequency over the next 50 years [243]. Therefore, we could conversely take advantage of this aerosol transmission route to establish the surveillance network by monitoring bioaerosols.

To further mitigate the indoor aerosol transmission risk, measures like better ventilation, improved bathroom circulation systems and plumbing system should be taken into consideration. Meanwhile, better personal protection and screening measures are needed, including masks with high filtration and comfort, human exhaled breath collection, exhaled volatile organic compound indicator analysis. These would help to reduce the emission and infection risks at the individual level, and help to improve the current swab-based screening approach. With these knowledge and technical improvements, we would be able to confidently deal with the next aerosol-transmission-related pandemic outbreak [146].

Antibiotic resistance microorganisms (ARMs) and antibiotic resistance genes (ARGs)

Microorganisms with antibiotic resistance naturally exist in the environment. However, the wide application of antibiotics has largely enhanced the background ARMs and ARGs [220,244]. ARGs have been widely found in the ambient air [9,245–247] and precipitation samples like rain and snow [248,249]. This means that these ARGs could transport through the air. Despite the air circulation on the global scale, heterogeneity of ARGs distribution has been observed on a global scale, suggesting a contribution from the local emission sources [250]. Transport of ARGs from different sources could directly result in the temporal dynamics of airborne ARGs in a certain region [251]. Correspondingly, it becomes a necessity to monitor the ARG hotspots, e.g., hospital, livestock and wastewater treatment plant.

Air pollution was found to be able to exacerbate the ARGs spatial spread as demonstrated by snow samples

from days of different air quality levels and different cities [252]. Additionally, it was found that the temporal ARGs pattern was also affected during a haze period [166].

Nowadays, in addition to air pollution, we face a number of problems, including the unequal economic and social development. These together result in the differential burdens of ARMs and ARGs on a global scale [253]. While under the frame of one health concept, it is of great importance to study how the airborne transmission route will affect the ARGs distribution patterns and their flow/exchanges among micro-organisms, plants, animals and humans [220]. To counteract the risk of ARGs transmission via airborne route, knowledge on the ARGs dynamics and fate in the air, their transferability to a new pathogenic host or even the human commensals, and the spillover risk from the known hotspots (e.g., hospitals, wastewater/ solid waste treatment plant, breeding farm) are needed.

Allergic disease associated with airborne allergens

Dispersion of biologicals into the air also causes allergies. Allergens in the air are one of the important factors in inducing allergic diseases on sensitized people. These aeroallergens are mostly proteins from pollen, fungi, animal fur, feces, and so on [254]. Here mainly pollen and their allergens were reviewed.

Dynamics and monitoring of airborne pollens

Concentrations of airborne pollen generally ranged from several to tens of thousands per cubic meter [255]. Allergenic pollen in the outdoor air mainly come from trees, grass and weeds, either passively under the wind disturbance or actively in a puffed mode [256]. The released pollen could disseminate horizontally on both short- and long-range distances. The distances that the pollen could travel depend on the pollen types [257]. Regarding a single isolated tree source, the transport distance of the released pollen is mostly related to the tree height and wind speed, resulting in more than 90% of the pollen deposition within a 50 m range [258]. The land cover could affect the local airborne pollen at a rather coarse 1–5 km meso-scale instead of a fine scale of 20–500 m [259]. Longer distance transport of pollen has been demonstrated by the non-local pollen found in the rainwater, and the unusual high birch level before the flowering [29,90].

Vertically, the pollen plume could be as high as 2 km [202]. Ground site was prone to be affected by the local sources in a pollen-specific manner [260]. This impact was also reflected in the differential daily temporary dynamics of pollens on the roof sites and on the ground sites [261]. Therefore, the land cover surrounding the site as well as the wind pattern need to be taken into consideration when considering the human exposure [262]. Currently, most pollen monitoring sites locate on the roof to improve the re-presentativeness and to avoid impact of local sources. The reasonability of the rooftop monitoring site was partly supported by a big data study covering nearly 60 monitoring sites [263]. This study reported that the height showed limited effects on the monitoring data. The diurnal patterns of various pollens differed in a type-specific manner [264]. Despite the varied spatial distributions of pollen sources, the exposure risk showed less spatial variability among allergic subjects [265].

Despite the strong need for pollen monitoring, airborne pollen counting methods still rely on the combination of gravimetric or volumetric sampler and the microscopic observation. The earliest monitoring of pollen which combined the air sampling and microscopy dates back to 1870s by Blackley in UK. Nowadays,

the majority of pollen monitoring sites locate in Europe and North America [266]. This is likely attributed to the high incidence of allergenic diseases in these areas (10%–40%) [267]. Under the current context of climate change, model work revealed that this population is assumed to increase continuously [268]. Due to the fact that modern people spend longer time indoors, indoor pollen dynamics also receive growing attention. Lower pollen levels indoors than outdoors have been reported, and the ratios appeared to depend on the human activity pattern [269].

However, the traditional approaches are time-consuming and labor-intensive. Automated real-time monitoring and forecast of airborne pollen is in strong necessity for the early-warning of allergenic populations. Recently, laser scattering [270] and automated image analysis [271] have been applied for pollen real-time monitoring. Combining this technique with certain machine learning algorithms, more than 100 automatic monitoring sites have been set in Japan [266]. Even mobile communication devices are proposed for allergy care [272]. In addition, Fourier transform infrared (FTIR) and Raman spectroscopy [273] and nuclear magnetic resonance analysis of pollen metabolites [28] have also been applied to improve the pollen taxonomic identification. Moreover, DNA-based sequencing technique has also been widely applied [274,275].

Additionally, pollen forecasts, including the start and end of pollen season, the spatial resolution, the concentration accuracy and the dispersal have been performed with various meteorological and biological parameters [276]. For instance, MOUDIS satellite greenness index, MERIS Terrestrial Chlorophyll Index, and Lidar have been applied [277,278]. Besides, combination of weather conditions and pollen count at the distributed stations have been applied to extrapolate the pollen count at non-monitoring sites with Gaussian Kriging interpolation method [279]. A prognostic model combining surface pollen count data, historical meteorological data, geography and vegetation data has been developed to simulate pollen concentrations [97].

Pollen allergy, air pollution and climate change

To induce pollen allergy, both intracellular allergens and adjuvants are necessary [222]. Of them, adjuvants function to trigger the immune system. The adjuvants usually include biogenic substances from pollen, microorganisms or other anthropogenic chemical compositions [222]. Therefore, any factors that could affect the pollen, the pollen allergenic protein or the adjuvants, would directly affect the allergic individuals.

Generally, the number of airborne pollens would be affected by the timing, duration and intensity of flowering especially [36,267,280]. In addition to the early laboratory evidence, increased durations of pollen season have been observed in the long time-series observation studies in San Francisco Bay area, southern Spain and Switzerland with temperature being a key factor [27]. In North America, anthropogenic climate change is proven to play a crucial role in lengthening the pollen seasons and increasing pollen counts [35]. Moreover, the impact of temperature has also been observed within a metropolitan city, as demonstrated by the flowering phenology of plants and the corresponding airborne pollen levels [281]. Early start of spring was significantly associated with the asthma hospitalizations in Maryland [282]. Taking birch tree as an example, model work revealed that birch tree would be differentially affected by future climate change under different scenarios [283]. However, no relationship has been reported between air pollutants (PM_{10}, $PM_{2.5}$, NO_x) and pollen count [284].

In addition to the intact pollen, the pollen allergenic proteins have received significant attention [285]. And growing evidence showed that pollen count might not be a good indicator for the allergen exposure risk [286]. Various factors affect the pollen rupture process in the air, including high humidity, mechanical friction, buildup of electrical charges, and lightning strike [287]. Rainfall was found to enhance pollen/spore rupture, resulting in large numbers of submicron particles [30,96,97,191,288,289]. Extreme weather conditions like thunderstorm could significantly affect the aeroallergens, which is well exemplified by the widely reported thunderstorm asthma phenomenon [290]. However, there is a large knowledge gap regarding the pollen allergen release process.

Notably, air pollutants have been linked to the pollen allergy via various pathways. On one hand, chemical modification of these aeroallergens, for instance, by ozone and NO_2, could possibly enhance their allergenicity [222,291,292]. On the other hand, air pollutants (e.g., diesel particles, fuel/biomass burning, secondary air pollutants and nanoparticles) likely serve as adjuvants in eliciting oxidative stress and inflammation [293–295]. Besides, microorganisms riding on the pollen possibly act as adjuvants in allergy development process [110,296]. To gain a further understanding on the effects of air pollution and climate change on allergies, some reviews can be referred to for more details [221,222,297].

In view of the current global trend of allergic diseases, more in-depth studies on the airborne transport of pollen, pollen allergen, and also other aeroallergens (e.g., fungi) are needed. From the point of atmospheric science, little is known about their transformation in the air and interaction with other components. Continuous monitoring of the aeroallergens including both the intact pollen and pollen allergens is necessary. Their transformation and the concurrent biological/chemical components in the atmosphere could directly affect the allergen and the associated adjuvants. Improved understandings on their atmospheric processes are necessary to explain the driving forces underlying the increasing allergenic diseases.

Non-communicable disease and microbiome

Except allergy, there are also various chronic inflammatory diseases (non-communicable disease). These diseases are likely associated with bioaerosol exposure with human microbiome as a modulator. These non-communicable diseases include chronic respiratory diseases (e.g., chronic obstructive pulmonary disease (COPD), asthma), cardiovascular diseases (e.g., heart attack, stroke), and cancers, which accounted for almost 71% of the global death [298].

Epidemiological evidence has linked air pollutants to the above adverse health effects, which were suggested to be mostly intermediated by oxidative stress and inflammatory effects [299,300]. As a part of atmosphere components, bioaerosols play a role by directly modulating the human inflammatory responses. The uniqueness of microorganisms lies in their capacity in activating the immune cells. Even after their death, several microbial debris (conserved components like endotoxins from gram-negative bacteria, glucan from fungi) still could activate the immune system by recognizing the pattern recognition receptors (PRRs) on immune cells. For example, endotoxins were found closely associated with the inflammatory response in various epidemiological and laboratory studies [301,302]. Moreover, the endotoxin signaling pathway was supposed to be affected by the oxidate potential associated with other PM components [303]. In addition, endotoxins on the pollen have been found to partly account for the pollen's allergenic potential [296]. Due to its natural property, biological components like endotoxins could not be manipulated or adjusted. However, it

would be necessary to identify the joint effects between bioaerosols and chemical components, which could help to provide more health-related targeted component control.

As the rapid development of sequencing techniques, our knowledge on the microorganisms has greatly improved. In addition to the pathogens, the role of microorganisms as a unity (referred to as microbiota or microbiome) in both humans and environments has received growing attention. Specially, microbiotas play a crucial role in modulating human immune system, which is closely related to various types of diseases, including both infectious and non-communicable diseases. Mounting evidence has suggested the role of human microbiome in non-communicable diseases [304]. Therefore, it is necessary to identify how the bioaerosol exposure affects human microbiome, especially those within the respiratory tract and skin [305]. Exposure to urban green space was found to be able to increase the human skin and nasal microbiome [306], which is likely modulated via bioaerosol exposure.

With the connotation of hygiene hypothesis gradually transforming from pathogen infection to the microbiome exposome [306], it is now becoming important to investigate how and to what extent the bioaerosol exposure will shape human microbiome [307]. As an unseen indispensable "organ" within human or environment, any disturbance on the microbiota homeostasis would have direct health effects on both humans or environment. Bioaerosols stand at the frontier interface between human, environment, and microbiota. To understand the effects of bioaerosol exposure on human health, knowledge on the impact of environmental change on bioaerosols and the impact of bioaerosol exposure on human microbiota (especially respiratory and skin microbiota) needs to be explored.

Conclusions and perspectives

In the epoch of Anthropocene, the impact of human activities on the earth system processes is becoming prominent via multiphase chemical pathways [308]. Meanwhile, the health of humans, animals, plants and environment is more interconnected and interdependent, belonging to "one health", in which microbiome likely plays a central role [141]. It is widely accepted that bioaerosols play a role in the atmosphere and could affect atmospheric processes, climate change and human health. As particles of biological origins, the ubiquitous bioaerosols are likely an unseen intersection between the atmosphere and biosphere, hydrosphere, cryosphere and lithosphere [309], which makes the bioaerosols at the nexus of air quality, climate system and human health. Therefore, it is time to revisit the role of bioaerosols in the earth system and their corresponding impacts on relevant entities.

Benefiting from the rapid development and reduced costs of high throughput sequencing techniques, it is clear that diversified microorganisms suspend in the air and could survive from long-range transport both vertically and horizontally. The frequent outbreak of haze air pollution has unveiled the searching on the function of bioaerosols in the air. Mounting evidence supported and verified the role of airborne transmission route in the development of COVID-19 pandemic. In addition, the relationships between bioaerosols and climate system, and the bioaerosol-associated allergenic, infectious and inflammation-related diseases were highlighted. However, there are yet many unknowns regarding the functional traits and impacts of bioaerosols.

Firstly, despite the persistence of viable microorganisms in the atmosphere, it is still unclear how and to

what extent the viable bioaerosols participate or modify the atmospheric chemical processes. Beyond their viability, it is of great importance to know their functional traits in the air. Moreover, it is necessary to elucidate the chemical and biological processes of bioaerosol transport in the atmosphere as well as their interaction with the atmospheric components. Subsequently, it is valuable to investigate whether the entire bioaerosol communities will affect the microbiome of each ecosystem (e.g., soil, ocean, plant) and how this impact is regulated by the atmospheric processes of bioaerosols. Experts from atmospheric science, microbiology and ecologist should work together to address this knowledge gap and integrate bioaerosols into the model of air quality and climate system for better prediction. Some long-lasting doubts in atmospheric chemistry might gain fresh understanding.

Secondly, it is necessary to establish the bioaerosol surveillance network on both local and global scales, in both outdoor and indoor environments, which is a great challenge. Due to climate change, the earth system is experiencing a great challenge, including the various systems on the earth. On one hand, surveillance of bioaerosols could give a hint of the change of the local ecosystem. On the other hand, it helps to provide an alert in terms of the emerging newly released pathogens, microorganisms with multi-antibiotic genes and allergens. To achieve this, an integrated monitoring system by combining advanced sampling and identification techniques of bioaerosols are urgently needed.

Thirdly, there are still yet many unknowns regarding the role of bioaerosols in human health. On one hand, further investigation on the chemical modification of the bioaerosols, joint effects of bioaerosol and air pollutants are in urgent demand. Moreover, alongside the recognition of microbiome in sustaining human health, it is important to move beyond the traditional cognition which is confined to the adverse effects of pathogenic/allergenic bioaerosols. It is time to elucidate how bioaerosol exposure will affect the human immune response and microbiome, e.g., respiratory microbiome and skin microbiome by integrating various omics techniques. In addition, a comprehensive understanding on the indoor bioaerosols becomes increasingly important due to the close relatedness between indoor and outdoor air and the long duration of modern people within indoor environment. Beyond the traditional practice to wipe out all indoor microorganisms, it is possible and necessary to re-shape and rewild the indoor microbial community for better building health.

Overall, many mysteries surround bioaerosols. Particularly, chemical and biological process of bioaerosols in the air, airborne transmission of emerging pathogens and allergens, association between bioaerosol exposure and development and variations of human microbiome and immune response have not been sufficiently studied and identified. A clear research momentum with bioaerosols is seen coming and well recognized. To address these questions, interdisciplinary studies need to be conducted to clarify the networks and synergies between bioaerosols and air quality, climate system and human health from micromolecular to macro-ecological level.

Conflict of interest

The authors declare no conflict of interest.

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