A Review on Airborne Microbes: The Characteristics of Sources, Pathogenicity and Geography

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Abstract: Microbes are widespread and have been much more studied in recent years. In this review, we describe detailed information on airborne microbes that commonly originate from soil and water through liquid–air and soil–air interface. The common bacteria and fungi in the atmosphere are the phyla of Firmicutes, Proteobacteria, Bacteroides, Actinobacteria, Cyanobacteria and Ascomycota, Basidiomycota, Chytridiomycota, Rozellomycota that include most pathogens leading to several health problems. In addition, the stability of microbial community structure in bioaerosols could be affected by many factors and some special weather conditions like dust events even can transport foreign pathogens to other regions, affecting human health. Such environments are common for a particular place and affect the nature and interaction of airborne microbes with them. For instance, meteorological factors, haze and foggy days greatly influence the concentration and abundance of airborne microbes. However, as microorganisms in the atmosphere are attached on particulate matters (PM), the high concentration of chemical pollutants in PM tends to restrain the growth of microbes, especially gathering atmospheric pollutants in heavy haze days. Moreover, moderate haze concentration and/or common chemical components could provide suitable microenvironments and nutrition for airborne microorganism survival. In summary, the study reviews much information and characteristics of airborne microbes for further study.

Keywords: airborne microbes; pathogens; transportation; atmospheric components; geographical characteristics

1. Introduction

Microorganisms (including bacteria, fungi and viruses) associated with atmospheric particulate matters, are known as bioaerosols. It has been reported that bioaerosols contribute up to 25% to atmospheric aerosols [1]. Furthermore, it is known that as an important contributor, chemical pollutants in the atmosphere may cause adverse human diseases with gathering in airborne particulate matters, especially respiratory illnesses. In addition to chemical pollutants, airborne microorganisms loaded in atmospheric particles have received growing attention in recent years due to the evidence supporting their role in the atmospheric environment and potential implications for human health, agricultural productivity and ecosystem stability [2–6]. Today, many pathogens are included in the microbial community in bioaerosols and may cause severe health problems, such as asthma, respiratory infections, skin and wound infections, acne and allergic reactions [7–9].

Besides, the sources of airborne microbes are mainly dominant by marine, soil and then followed by microbe dispersal in some processing plants depended on role of microorganism. For instance,
many studies have proved that airborne microbes had the same characteristics and structure with marine and soil [10]. Droplet diffusion in composting plants, waste treatment plants and sewage treatment work—which mainly rely on bacteria and fungi to degradation and disposal—also contributes to increase the levels of microorganisms to the atmosphere [11,12]. The species of bacteria and fungi in bioaerosols are abundant and multiple. The common microbial phyla including *Firmicutes*, *Proteobacteria*, *Bacteroides*, *Actinobacteria*, *Cyanobacteria*, *Ascomycota*, *Basidiomycota* and *Chytridiomycota*, which have been proven to contain numerous pathogens. However, the stability of microbial community structure could hardly to maintain for a long time, as microbial living conditions in the atmosphere is inconstant (for example, relative humidity, temperature, light, chemicals, nutrition, etc.) under different meteorological parameters. Furthermore, the community structure tends to differ with the variation of survival conditions in different locations and regions they grow [13–15]. Therefore, as airborne microbes are mainly loaded in particulate matters in the atmosphere, the increased concentration of particulate matters in special weather conditions (dust event and haze days) will lead to greatly high levels of microbes [16–18]. However, due to the enriched atmospheric pollutants (PAHs, heavy metals, etc.) in particulate matters, the number of airborne microbes in heavy hazy days tends to decrease.

In this review, we describe the characteristics and transport behaviors of airborne microorganisms and the behaviors of pathogens in the atmosphere.

2. The Sources and Characterization of Airborne Microbes

The spread of microorganisms from liquid systems or soil (e.g., *Bacillus* *bataviensis*, *Sphingomonas*, *Arcobacter*) to the atmosphere is attributed to the dispersal of air current and droplets, which is the best explanation to the presence of some specific microorganisms presented in totally different environments (Table 1) [16,19–26]. In some studies, the only microorganism identified in the Antarctica soil was *Brevundimonas* sp., while *Sphingomonas* was in the Antarctic dust [24,27]. The microbial sources and communities structure in the eolian dusts of Southern Australia were studied [28], and the result showed that the microorganisms in saline lake sediments and biological soil crusts are the origin [29]. A highly diverse and abundant bacterial community was presented, due to the spread of air masses in an intense Saharan dust event [16]. Composting is a process based on the degradation of wastes by microbial activity. Many different bacteria and fungi are released during compost processing (fresh waste delivery, shredding, compost–pile turning and compost screening) [23,25]. The bacterial community structure studied in a wastewater treatment plant showed that the composition of microorganisms in water was one of the most important sources of bacterial community in bioaerosols [30]. Furthermore, plants and soil were also found to major sources of the airborne bacteria in aerosols [26]. Marine systems are the best survival environments for microorganism and includes millions of species of bacteria, fungi and minor protozoans [31]. In fact, aerosols and droplets created from the surface of aquatic systems are known to enrich and convey microbes through the liquid–air interface [21,32]. There are studies demonstrating that most microorganisms belonging to marine systems have been found in non–liquid environments [21,33]. In addition, the variability of airborne bacteria observed in urban Mediterranean area (Thessaloniki, Greece) showed that some species possibly originated from marine origin (e.g., *Synechococcus* sp.), while most species were from soil and wastewater origin [34].
Penicillium cyanobacteria actinobacteria bioaerosol samples, including the genera of phyla common bioaerosols of urban and subway area, the microbial community is mainly consisted by the reports, not only including pathogens also with common bacteria and fungi in bioaerosols. In the strong solar radiation, oxidants and loaded by particulate matters in the air that contain some hydrogen peroxide, radicals, which are potentially affecting the growth of microbial organisms [35]. However, despite these severe conditions, a considerable fraction of airborne microbes remains alive and maintains their activity. There are numerous species of airborne microbes tested in various conditions under different regions and weather conditions (like sunny, cloudy or rain, etc.) [5].

Atmosphere Particulate Matters (PM) on Airborne Microbes

In fact, the conditions in the atmosphere are unfavorable for microorganisms, due to lack for nutrition and moderate survival microenvironment. For instance, microbial cells need to tolerate strong solar radiation, oxidants and loaded by particulate matters in the air that contain some hydrogen peroxide, radicals, which are potentially affecting the growth of microbial organisms [35]. However, despite these severe conditions, a considerable fraction of airborne microbes remains alive and maintains their activity. There are numerous species of airborne microbes tested in various reports, not only including pathogens also with common bacteria and fungi in bioaerosols. In the common bioaerosols of urban and subway area, the microbial community is mainly consisted by the phyla Fungi (Thermoactinomyces, Bacillus, Staphylococcus, Streptococcus, Abiotrophia), Alpha- and Betaproteobacteria (Acinetobacter, Stenotrophomonas, Pseudomonas, Sphingomonas, Massilia, Delftia, Brevundimonas), Bacteroides (Empedobacter, Pontibacter, Adhaeribacter, Hymenobacter), Actinobacteria (Thermobifida, Streptomyces, Kitasatospora, Propionibacterium, Friedmanniella) and Cyanobacteria (Cranium) [34,36–42]. Compared to bacteria, the fungi species also were found in bioaerosol samples, including the genera of Aspergillus (A. fumigatus, A. niger, A. ochraceus, A. sydowii), Penicillium, Alternaria, Epicoccum, Fusarium, Cladosporium, Rhizopus and Mucor, Thermoactinomyces, etc. [25,39,43–46]. In special haze weather, the increased microbial species include microorganisms from the genera of Methylobacillus, Tumebacillus, Desulfurispora, Okdonella, Caenimonas, Geminicoccus, Sphingopyxis, Cellulomonas and Rhizobacter [47], due to the increased levels of particulate matters. Furthermore, the microbial community structure during Asian dust events clearly was distinguished from that on non-Asian dust days [48,49], as the additional transported foreign microorganisms caused by strong wind. For example, the genera Bacillus and Modestobacter were increased about 3-fold, while Escherichia–Shigella was decreased significantly during dust events [50].

3. The Effect of Atmospheric Particulate Matters (PM) on Airborne Microbes

As is known that the particulate matters (PM) are distinguished into two sorts according to particular diameter, fine particulates PM2.5 (diameter <2.5 μm) and coarse particulates PM10 (diameter between 2.5–10 μm) [17]. Generally, most airborne microorganisms are loaded by PM in the atmosphere, and numerous studies have studied the relationship between microbial quantity and particulates diameters [6]. In PM, the range of dynamic diameter can be distinguished into six stages, ≥7.0 μm (Stage 1), 7.0–4.7 μm (Stage 2), 4.7–3.3 μm (Stage 3), 3.3–2.1 μm (Stage 4), 2.1–1.1 μm (Stage 5) and 1.1–0.65 μm (Stage 6). The greatest proportion of airborne bacteria were detected on Stage 3 (3.3–4.7 μm) [51], which had the similar results with other studies [52,53]. It was further proved in other works that the size distribution of microbes presented an increase in fine PM on hazy days and an increase in coarse PM on foggy days, while presented one peak at 1.1–2.1 μm and another peak at 4.7–7.0 μm on sunny days [54]. The size distribution of airborne microbes was studied under severe haze periods, which showed various bacterial concentration in PM1.18–2.6 7314 cells/m³), PM1.18–0.32 (7212 cells/m³) and PM0.36–1 (6982 cells/m³) [6]. However, the fungi have variety of highest proportion in various stages under different regions and weather conditions (like sunny, cloudy or rain, etc.)
The highest number of fungi with aerodynamic diameter ranging from 2.1 to 3.3 μm were associated with coastal areas of bioaerosols [56]. It was revealed that the phenomenon that the quantities distribution of common fungi in PM10 and PM2.5 are diverse in an urban area, as different size fractions and chemicals (pollutants, O₃, SO₂ and NO₂) in two types of particulate matters [43]. Therefore, the concentration of microorganisms in different PM diameters has significant effects on the study of microbial community in bioaerosols, due to the application of sampling devices when collecting bioaerosol samples [57].

Furthermore, some chemical components in PM provide a media for airborne microorganism attachment—as well as a suitable microenvironment for their growth and survival in the air (Table 2). Recently, many studies are focused on the relationship between chemicals of PM and airborne microbes. One of studies reported that the bacterial community structure was most positively related to water–soluble ions and metal elements (SO₄²⁻, NO₃⁻, NH₄⁺, K⁺ and Cl⁻), which indicated that these aerosol particles were of great significance on the bacterial compositions [58]. However, the effects of air pollutants on the atmospheric microbial community in heavy haze contaminated areas were found to decrease the abundance and richness of airborne microbes by restraining the growth of bacteria [46]. Besides, chemical components/pollutants in atmospheric PM were key factors that significantly altered the bacterial concentrations and community compositions [17]. The number of total airborne microbes appeared to increase firstly with the increased concentration of PM accumulation in the air, while began to decrease in severely polluted condition with greatly higher haze concentration [59]. Therefore, it is noteworthy that the competition between toxic effect and growth promotion components may contribute to this result, due to chemical pollutants adhering to PM. As discussion above, moderate concentration of particulate matters (PM) in the air bring about an increased concentration of microorganisms, such as in low–hazy, low–foggy and/or low–smog condition, in which some chemicals did not increase to sufficient quantities to cause noxious effects. However, in heavy air pollution and with considerably higher PM quantities gathering, the growth–promoting effect of the augmented levels of toxic and hazardous chemicals (sulfate, nitrate, polycyclic aromatic hydrocarbons (PAHs), etc.) greatly suppress the survival of microbes. Some studies have found that quantities of some heavy metals (like Pb, Zn, As) and PAHs in PM were about 3–8–fold higher during serious haze events than those on no haze days [60,61]. What is more, another study also revealed that the concentration of bioaerosol ascended once upon the haze occurrence and then decreased as the chemicals enriched in PM in the later periods of haze event [62]. It was found that the culturable bacteria and fungi had lower levels on severe haze days than on non–haze days [18].

Table 2. Factors that influence the characteristics of airborne community.

| Factors | Ways |
|---------|------|
| Particulate matters in hazy/foggy weather | Formaldehyde, O₃, H₂O₂, PAHs | Noxious effects on microbial growth |
| | Water–soluble ions, organic carbon | Provide habitat and nutrients for microbes |
| | Strong acids | Noxious effects |
| Strong solar radiation (UVs) | | Noxious effects |
| Temperature (relative humidity) | | Provide comfortable survival environment |
| Dust | | Carry microbes to far distances |
| Thunderstorm | | Uplift microorganisms in altitude above the tropopause |
4. The Effect of Airborne Microbes on the Environment

Numerous studies have focused on studying airborne microorganisms, as some of microbes in bioaerosols are considered as serious risk factor for health problems [63]. Table 3 lists the various types of airborne pathogenic microorganisms brought about health problems to human, plants and mammals. First, respiratory diseases caused by exposure to bioaerosols include aspergillosis in immunocompromised individuals, extrinsic allergic alveolitis, allergic rhinitis, asthma, upper airway irritation and mucous membrane irritation [64]. Brodie et al. revealed the consistent presence of pathogenic bacteria members in urban aerosol [20], in which bacteria from Arcobacter, Helicobacter, tick–borne Rickettsia, Clostridium botulinum type C, Burkholderia mallei, Burkholderia pseudomallei appear to be noxious for environment with leading to human health disease and mammals illness (for example, bacteremia, gastrointestinal, gastric ulcers, glanders and melioidosis) [12]. In their study, the samples were conducted from urban area of two U.S. cities, which indicated that many pathogenic microorganisms existed in urban area and had possibility to pose health threaten to city residents. Bioaerosol samples were studied from three main Chinese regions (Beijing, Tianjin and Hebei province) [26], where all experienced severe atmospheric pollution area usually. The study proved almost 18 pathogens species, among which, the dominant Escherichia coli could result in urinary tract infections, diarrhea, hemorrhagic colitis and hemolytic–uremic syndrome in humans [65]. The Staphylococcus epidermidis, a causative agent of implanted prostheses infections (e.g., heart valves and catheters), also dominated in the air. Besides, Propionibacterium acnes and Enterococcus faecium are known to cause acne and nosocomial infections, respectively [2,65,66]. The genera of Pseudomonas and Acinetobacter were tested in the urban area of Thessaloniki City [34] as well, which are known to cause respiratory infections and pneumonia, skin, wound infections, respectively [67,68]. In addition, Staphylococcus and Ralstonia [69,70] all accounted for mainly portions among the tested genera in bioaerosols, which are pathogen to human and plants, respectively [71]. There are several other pathogens detected in bioaerosols, as shown in Table 3 [72–76].
Table 3. Pathogens detected in different bioaerosols.

| Phyla          | Pathogen                      | Potential Pathogenicity                                                                 | Host                  | Literature |
|----------------|-------------------------------|----------------------------------------------------------------------------------------|-----------------------|------------|
| Firmicutes     | *Streptococcus gallolyticus*  | pharyngitis, pink eye, meningitis, pneumonia, endocarditis, erysipelas, necrotizing fasciitis | Human                 | [26]       |
|                | *Streptococcus mitis*         |                                                                                        |                       |            |
|                | *Staphylococcus*              | food poisoning, herpetic and exfoliative dermatitis                                      | Human                 | [69,71]    |
|                | *Bacillus circulans*          | sepsis, bacteremia, abscesses, meningitis                                              | Human                 | [41,42]    |
|                | *Enterococcus faecium*        | nosocomial infections                                                                    | Human                 | [65]       |
|                | *Staphylococcus epidermidis*  | infections of implanted prosthesis (e.g., heart valves and catheters)                   | Human                 | [26]       |
| Proteobacteria | *Arcobacter*                  | bacteremia, gastrointestinal illness                                                    | Human                 | [20]       |
|                | *Helicobacter*                | gastric ulcers                                                                          |                       |            |
| Gamma–proteobacteria | *Enterobacter cloacae*        | potential infections of soft tissue, urinary tract and respiratory                       | Human                 | [26]       |
|                | *Pseudomonas aeruginosa*      | nosocomial infections                                                                    | Human                 | [34]       |
|                | *Aeromonas hydrophila*        | release exotoxin to cause enteral infections                                             | Human                 | [26]       |
|                | *Enterococcus casseliflavus*  | respiratory infections                                                                   | Human                 | [34]       |
|                | *Enterococcus haimoperoxidus* | urinary tract                                                                           | Human                 | [26]       |
| Gamma–proteobacteria | *Acinetobacter*              | pneumonia, skin and wound infections                                                    | Human                 | [7,67]     |
| Actinobacteria | *Propionibacterium acnes*     | acupuncture                                                                             | Human                 | [2]        |
|                | *Thermoactinomyces vulgaris*  | hypersensitivity–induced pneumonitis                                                    | Human                 | [9,25,72]  |
|                | *Saccharopolyspora reieivigula* | alveolitis, bronchial asthma                                                              |                       |            |
| Proteobacteria | *Klebsiella pneumoniae*       | mucormycosis, organic dust toxic syndrome (ODTS)                                         | Human                 | [73]       |
|                | *Aspergillus fumigatus*       | mucormycosis                                                                            | Human                 | [74]       |
|                | *Bjerkandera adusta*          | chronic cough                                                                            | Human                 | [75]       |
| Ascomycota     | *Cryphonectria parasitica*    | chestnut blight                                                                         | Human                 | [75]       |
| Basidiomycota  | *Puccinia melanocephala*      | sugarcane rust                                                                           | Plants                | [3]        |
| Gamma–proteobacteria | *Escherichia coli*         | diarrhea, sepsis                                                                         | Infantic, immature livestock | [26]       |
| Firmicutes     | *Clostridium botulinum Types C* | release exotoxin to cause disease                                                       | Mammals, fish, birds  | [20]       |
| Alpha–proteobacteria | *Burkholderia mallei*        | glanders                                                                                | Mammals               |            |
| Beta–proteobacteria | *Burkholderia pseudomallei*  | melioidosis                                                                             |                       |            |
| Firmicutes     | *Bacillus sp.*                | biodeterioration                                                                        | Mural paintings       | [76]       |
| Heterokontophyta | *Phlyophthora infestans*      | potato late blight                                                                       | Plants                | [3]        |
| Ascomycota     | *Cryptonectria parasitica*    | chestnut blight                                                                          |                       |            |
| Basidiomycota  | *Puccinia melanocephala*      | sugarcane rust                                                                           |                       |            |
| Beta–proteobacteria | *Ralstonia*                  | a plant pathogen                                                                        |                       |            |
Some special plants and/or working environment all would release numerous numbers of bioaerosols within some pathogenic bacteria including Actinomycetes and fungi. For instance, bioaerosols released from composting plants have cause greatly concern due to their potential impacts on health of worker and public living closely to composting facilities. The biological hazards emission from composting activities usually include fungi, bacteria and endotoxin [77]. Le Goff et al. sampled at five French composting plants, in which the dominated fungi and bacteria were \textit{Penicillium} sp., \textit{Aspergillus fumigatus}, \textit{Thermomyces lanuginosus}, etc. and \textit{Bacillus} sp., \textit{Geobacillus thermodenitrificans}, \textit{Saccharopolyspora rectivirgula}, etc., respectively [25]. \textit{Aspergillus fumigatus}, which is an opportunistic fungal pathogen, may cause invasive aspergillosis in immuno–weak individuals under long–term exposure [11,44]. Besides, \textit{Thermoactinomyces vulgaris} and \textit{Saccharopolyspora rectivirgula} are associated with hypersensitivity induced pneumonitis and other allergies like alveolitis and/or bronchial asthma [9,72]. The airborne microorganisms may also be able to survive by long–distance transport in the atmosphere, thus some pathogens release from the composting process lead to greatest concern [78]. Besides, livestock farms are also known to emit large amounts of bioaerosols [79] and working or residing at closely areas with high gathering of livestock farms are easily to develop severe respiratory health problems [80–82]. The microbiome composition in bioaerosol originated from livestock farms was conducted, in which several potential pathogens were identified, such as \textit{Streptococcus bovis}, \textit{Serratia entomophila}, \textit{Aerococcus viridans} and \textit{Corynebacterium xerosis}, which are considered as infectious agents in human skin, lung, and/or the urinary tract infections for (feeble) individuals [36]. Furthermore, once people expose to high density of bioaerosols, they are more likely to develop organic dust toxic syndrome (ODTS), which includes a series of human illnesses, namely, mucormycosis, respiratory, urinary tract and gastroenteric tract infections and results from pathogens such as \textit{Klebsiella pneumoniae}, \textit{A. fumigatus}, \textit{Rhizopus microspores}, \textit{Erwinia Klebsiella}, \textit{Enterococcus caselliflavus}, \textit{Enterococcus haemoperoxidus} and \textit{Acinetobacter baumannii}, respectively [74,83].

Pathogens of airborne microbes lead to diseases or allergic reactions and thus cause serious attention. Actually, people who expose to some special working environment, are more likely to develop illness discussed above. For example, people who work in mineral processing, agricultural and food processing, waste solid or water treatment factories have greatly possible to get diseases caused by pathogenic microorganisms. Besides, in special atmospheric conditions (dust event and haze days), the chance that human obtains health disease will increase to some extent. In addition to human beings, livestock, mammals and other matters in environment (plants, agricultural crops, statues, paintings, etc.) also will be ill caused by airborne microbes. \textit{Bacillus decolorationis} sp. nov. was revealed to be responsible for the biodeterioration to mural paintings with causing discoloration on paintings [76]. Moreover, the plants also suffered from diseases, causing by microorganism in the atmosphere [3].

Besides, some studies have revealed that the microorganisms in bioaerosols could indirectly influence global climate and atmospheric processes [84–86]. For instance, airborne microorganisms contribute to participating in numerous atmospheric physicochemical processes: the formation of cloud droplet, precipitation, ice nucleation and the degradation of chemical compounds in cloud water [4,87,88]. Specific species of bacteria, fungi and plankton were reported to act as ice nuclei and are responsible for initiating the ice clouds formation [89,90] and found that ice nucleation activity of ice nuclei consisted by microorganisms is better than those of inorganic substances. Actually, bacteria and fungi that composed ice nucleation active proteins can increase the temperature of initiating ice formation at warmer than \(-5 \, ^\circ\text{C}\) [91], while high temperature tends to decrease the activity of ice nuclei synthesized by inorganic matters. In addition, the ice nucleation activity of fungi and lichen could keep stable at temperatures up to \(60 \, ^\circ\text{C}\) [92–94]. It was found that the ice nucleation active genera \textit{Xanthomonas} even holds much of their ice nucleation activity at temperatures as many as \(105 \, ^\circ\text{C}\) [5] and also revealed that the ice nucleation activity of pollen is not influenced by increasing temperature treatment at about \(100 \, ^\circ\text{C}\) [95].
5. The Geographical Characteristics of Airborne Microbes

The earth’s atmosphere is an extreme environment for microbial life, as it has low levels of nutrients, but strong UV radiation that could prevent microbial survival. However, the behavior and habit of microbial community in aerosols are rarely predictable and describable. There are various factors (relative humidity, temperature, season, special weather conditions: haze and dust, etc.) in the atmosphere, which have much possibility to influence microbial abundance. Thus, to study and figure out microbial composition and how it varies with different atmospheric factors, geographical characteristics has great significance.

The microbial concentration and community structure could hardly maintain stability in bioaerosol for a long time, due to the air masses and various meteorological conditions. It is known that the microbial concentration varies with different seasonal characteristics. The concentration of total microbes in the atmosphere appeared to the highest quantity in winter and the lowest in summer [54], as serious hazy and foggy weather emerging with higher particulate matters becoming inhabitants for microorganisms. There are various factors that influence microorganism activity in bioaerosols [96] and its results of principal component analysis (PCA) indicated that the season, haze levels, and sampling periods are mainly associated with influencing on bioaerosols. The lowest bacterial concentration of $7.05 \times 10^2 \pm 4.74 \times 10^2$ CFU/m$^3$ were detected in summer season in by researchers [56,97], attributing to the high intensity of solar radiation [98], high ozone and high temperature (Tang, 2009). In addition to various seasons, meteorological factors also influence the microbial concentration. It was found that several atmospheric factors cause stress to the survival of microorganisms in bioaerosols with freeze–thaw appeared to be the greatly stronger factor, followed by oxidants and solar light, which had limited impacts on microorganism survival as well [99].

According to other studies, temperature had the strongest correlation with bacterial community composition [10,43,47,100]. However, relative humidity showed negative relationship with fungi [101], while there was no relationship of fungal concentration with solar radiation [102]. Nevertheless, the almost opposite conclusions and results in different reports may be because of various sampling locations and periods. Further, this trend of seasonal characteristics considerably is various under different locations or regions, as the levels of particulate matters and meteorological parameters are different. The concentration of microorganisms in bioaerosols are list in Table 4, which shows that the concentration in different locations and regions. The details on how various factors influence the diversity of microorganism and microbial composition in the atmosphere were provided in other study [39]. In their study, authors proved that geographic location, season and local climate influence the microbial communities, in which location accounted for large proportion on influencing the bacterial community composition. The highest bacterial abundance was recorded during summer in other study as well [34], but no significant seasonal differences were found between summer and winter in Thessaloniki, Greece. Additionally, higher quantities of microorganisms were revealed in autumn–winter in Qingdao, China [56], while relatively high levels of airborne bacteria were found in both fall and spring seasons in northern Colorado, USA as well [103].

Another remarkable example on airborne fungal spore was reported from more northerly location in Stockholm where low winter temperatures significantly decreased spore concentrations and a snow cover caused a drop to even zero level [104]. Therefore, it is significantly important to enhance our comprehension of how various factors shape the abundance and composition of airborne microbes in different environments by studying spatial and temporal differences [15]. For example, the distribution of airborne microbes with elevation was studied in an Asian dust downwind area [105], in which concentrate microorganisms from continental and marine areas carried by the westerly winds. Moreover, the study shows that the bacterial community (e.g., Bacillus, Actinobacterium species) primarily consisted of terrestrial bacteria at the altitude of 3000 m. On contrast, at 1000 m and 10 m, those included marine bacteria (e.g., the classes Cyanobacteria and Alphaproteobacteria). Besides, another study conducted in a high elevation research station showed that bacterial abundances varied from season (the highest concentrations in fall and spring) and consistent with the changes in total particle concentrations as previously mentioned [103].
Compared with seasonal features, the characteristics and concentration of microorganism tend to show considerable variations during special weather conditions (like dust, haze, monsoon, thunderstorm, etc.). It had been demonstrated that microbial community structures could be altered by long-range and/or short-range transport [13,14], especially under dust events. The dust event could transport pathogenic microorganisms [106], such as allergen burden and asthma [75] and possibly lead to the dispersal of diseases such as Kawasaki disease in humans [107] and rust diseases in plants [3]. *Bacillus circulans* was found to transported during dust event, which is reported to cause sepsis, bacteremia, abscesses and meningitis in humans [50]. Besides, the bacterial abundance in dusty and non-dusty weather condition indicated that the bacterial abundance on Asian dust days was considerably increased by approximately five-fold (from 2 ± 3 × 10^3 to 1 ± 0.6 × 10^4 cells/m^3) [48]. In addition to dust weather, the haze and foggy weather conditions also exert great effects on microbial characteristics in bioaerosols [47,54]. What is more, thunderstorm have been studied to exert influences on airborne microbes. It was proved by the presence of microorganisms (e.g., *Deinococcus, Staphylococcus, Brevibacterium*), which were collected and isolated in stratosphere of atmosphere [108,109]. Numerous bacteria including Actinomycetes and fungi living in about 20–50 km elevation (e.g., *Actinobacteria, Bacillus spp., Actinomyces sp., Halorubrum lacusprofundi* etc.) were reviewed in other study [110]. Furthermore, the existence of microorganisms in high elevation ascribing to thunderstorm event was also reported [111], as microorganisms could carry high internal electric charges [112] and under thunderstorms, the strong electric fields could expedite charged microbes particulates rapidly up into high altitudes [113–117].

| Concentration (cfu/m^3) | Regions | Sites | Literature |
|-------------------------|---------|-------|------------|
| (bacteria) 565 ± 464    | Xi’an, China | nearby city major roads | [51] |
| (fungi) 399 ± 371       |         |       |            |
| (bacteria) 81 ± 31      | Seoul, Korea | building (out) | [113] |
| (fungi) 96 ± 45         |         | forest |            |
| (bacteria) 125 ± 51     | Beijing, China | building (out) | [53] |
| (fungi) 253 ± 121       | Jeddah, Saudi Arabia | university campus | [43] |
| (bacteria) 1110 ± 976   | Beijing, China | roof of a building | [115] |
| (fungi) 45–591          | Cincinnati | homes area | [116] |
| (fungi) 800            | Graz, Austria | city center | [97] |
| 1344                   | Brisbane, Australia | indoor school | [114] |
| (bacteria) (heavy hazy) 224 ± 186 | Beijing, China | / | [117] |
| (non-hazy) 358 ± 349    |         |       |            |
| (fungi) 0–3882          | Cincinatti Americ | / |            |
| (bacteria) 0–2500       | Graz, Austria | city center | [97] |
| (bacteria) (downtown) 1700 ± 595 | Tijuana, Mexico | / | [117] |
| (bacteria) (River valley) 40,100±21,689 | / | / |            |
| Concentration (cells/m^3) | Thessaloniki, Greece | city center | [34] |
| (summer) 12 × 10^4       | Xi’an, China | urban area | [59] |
| (winter) 8.4 × 10^4      |         |       |            |
| (spring) 2.38 × 10^5     |         |       |            |
| (summer) 1.66 × 10^6     | Qingdao, China | roof of a campus building | [54] |
| (autumn) 4.22 × 10^5     |         |       |            |
| (winter) 6.77 × 10^6     | Osaka, Japan | downtown area | [48] |
| (hazy) 7.09 × 10^6       |         |       |            |
| (foggy) 9.00 × 10^6      |         |       |            |
| (non-hazy) 6.55 × 10^6   |         |       |            |
| (dust) 1 ± 0.6 × 10^4    |         |       |            |
| (non-dust) 2 ± 3 × 10^4  |         |       |            |
| (hazy) 6.12 × 10^6 ± 3.50 × 10^6 | Xi’an, China | urban area | [59] |
| (non-hazy) 2.15 × 10^6 ± 1.26 ×10^6 | / | / | |

Thus, due to the transported microorganisms from external regions, the indigenous microbial community structure may be impacted by foreign microorganisms. For instance, microbial...
community tend to have a competition for resources (e.g., nutrients) [118]. It was revealed that microbes in aeolian dust may have a greater impact on indigenous microbial communities in the downwind areas near the dust source [119]. There could exist two causes accounting for the increase of airborne microbial concentration on hazy days. First, some atmospheric factors including temperature, relative humidity, and the concentration of atmospheric chemicals like PM2.5, PM10, NO2 and SO2, etc. were higher on hazy days than on non–hazy days. Secondly, the stable stratification and lower wind velocity on hazy days created an adverse environment for the dispersion of particulate matter, which provide more comfortable environment for airborne microbes. However, although most studies showed that the haze days event could increase the microbial abundance, the study proved that higher PM2.5 concentration may cause lower bacterial richness and diversity during heavy haze days [58], due to that there are numerous chemical pollutants and secondary pollutants in severe haze atmosphere, which could restrain the growth of airborne microbes. No matter how haze days could bring about more nutrition or chemical pollutants for airborne microbes to increase or decrease its concentration, the possible reason for such conditions is that the concentration and characteristics of airborne microbes are various with different locations and regions, as discussed above.

6. Conclusions

In conclusion, although the atmosphere is such an adversity environment for the growth of airborne microbes, the richness and abundance of microorganism is very high in the air. Moreover, almost all are loaded in particulate matters (PMs), thus the size distribution of PMs may influence the microbial community structure in various range of particles diameters. However, the microorganisms surviving in aerosols also may be affected by different factors (for example, meteorological parameters, the concentration of PMs, sampling locations and periods, etc.). Moreover, it has been demonstrated that the special weather conditions like dust events, haze and foggy days will affect microbial community structure and microbial concentration, especially on indigenous microbes. In fact, it is the truth of numerous pathogenic microorganisms have caused much attention, and most are able to transport by strong wind speed like under dust events. Therefore, these pathogens could lead to severe health problems to human, animals and even plants with greatly wide range in the air. In words, the more information of airborne microbes (especially pathogens) the more measures and studies we could conduct.

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References

1. Jaenicke, R. Abundance of cellular material and proteins in the atmosphere. *Science* 2005, 308, 73, doi:10.1126/science.1106335.
2. Bojar, R.A.; Holland, K.T. Acne and Propionibacterium acnes. *Clin. Dermatol.* 2004, 22, 375–379, doi:10.1016/j.clindermatol.2004.03.005.
3. Brown, J.K.M.; Hovmøller, M.S. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* 2002, 297, 537–541.
4. Delort, A.-M.; Vaïtilingom, M.; Amato, P.; Sancelme, M.; Parazols, M.; Mailhot, G.; Laj, P.; Deguillaume, L. A short overview of the microbial population in clouds: Potential roles in atmospheric chemistry and nucleation processes. *Atmos. Res.* 2010, 98, 249–260, doi:10.1016/j.atmosres.2010.07.004.
5. Hill, T.C.; Moffett, B.F.; Demott, P.J.; Georgakopoulos, D.G.; Stump, W.L.; Franc, G.D. Measurement of ice nucleation-active bacteria on plants and in precipitation by quantitative PCR. *Appl. Environ. Microbiol.* 2014, 80, 1256–1267, doi:10.1128/AEM.02967-13.
6. Xu, C.; Wei, M.; Chen, J.; Wang, X.; Zhu, C.; Li, J.; Zheng, L.; Sui, G.; Li, W.; Wang, W.; et al. Bacterial characterization in ambient submicron particles during severe haze episodes at Ji’nan, China. *Sci. Total Environ.* **2017**, *580*, 188–196, doi:10.1016/j.scitotenv.2016.11.145.

7. Dijkstra, L.; Nemec, A.; Seifert, H. An increasing threat in hospitals: Multidrug-resistant Acinetobacter baumannii. *Nat. Rev. Microbiol.* **2007**, *5*, 939–951, doi:10.1038/nrmicro1789.

8. Nazaroff, W.W. Embracing microbes in exposure science. *J. Exp. Sci. Environ. Epidemiol.* **2019**, *29*, 1–10.

9. Lacey, J.; Crook, B. Fungal and actinomycte spores as pollutants of the workplace and occupational allergens. *Ann. Occup. Hyg.* **1988**, *32*, 515–533.

10. Niazi, S.; Hassanvand, M.S.; Mahvi, A.H.; Nabizadeh, R.; Alimohammadi, M.; Nabavi, S.; Faridi, S.; Dehghani, A.; Hoseini, M.; Moradi-Joo, M.; et al. Assessment of bioaerosol contamination (bacteria and fungi) in the largest urban wastewater treatment plant in the Middle East. *Environ. Sci. Pollut. Res. Int.* **2015**, *22*, 16014–16021, doi:10.1007/s11356-015-4793-z.

11. Taha, M.P.M.; Drew, G.H.; Longhurst, P.J.; Smith, R.; Pollard, S.J.T. Bioaerosol releases from compost facilities: Evaluating passive and active source terms at a green waste facility for improved risk assessments. *Atmos. Environ.* **2006**, *40*, 1159–1169, doi:10.1016/j.atmosenv.2005.10.110.

12. Wesley, I.V.; Wells, S.J.; Harmon, K.M.; Green, A.; Schroeder-Tucker, L.; Glover, M.; Siddique, I. Fecal shedding of Campylobacter and Arcobacter spp. in dairy cattle. *Appl. Environ. Microbiol.* **2000**, *66*, 1994–2000.

13. An, S.; Couteau, C.; Luo, F.; Neveu, J.; DuBow, M.S. Bacterial Diversity of Surface Sand Samples from the Gobi and Taklamakan Deserts. *Microb. Ecol.* **2013**, *66*, 850–860, doi:10.1007/s00248-013-0276-2.

14. Puspitasari, F.; Maki, T.; Shi, G.; Bin, C.; Kobayashi, F.; Hasegawa, H.; Iwasaka, Y. Phylogenetic analysis of bacterial species compositions in sand dunes and dust aerosol in an Asian dust source area, the Taklimakan Desert. *Air Qual. Atmos. Health* **2016**, *9*, 631–644.

15. Ladau, J.; Eloe-Fadrosh, E.A. Spatial, Temporal, and Phylogenetic Scales of Microbial Ecology. *Trends Microbiol.* **2019**, *27*, 662–669, doi:10.1016/j.tim.2019.03.003.

16. Federici, E.; Petroselli, C.; Montalbani, E.; Casagrande, C.; Ceci, E.; Moroni, B.; la Porta, G.; Castellini, S.; Selvaggi, R.; Sebastiani, B.; et al. Airborne bacteria and persistent organic pollutants associated with an intense Saharan dust event in the Central Mediterranean. *Sci. Total Environ.* **2018**, *645*, 401–410, doi:10.1016/j.scitotenv.2018.07.128.

17. Cao, C.; Jiang, W.; Wang, B.; Fang, J.; Lang, J.; Tian, G.; Jiang, J.; Zhu, T.F. Inhalable microorganisms in Beijing’s PM2.5 and PM10 pollutants during a severe smog event. *Environ. Sci Technol.* **2014**, *48*, 1499–1507, doi:10.1021/es4048472.

18. Hu, L.-F.; Zhang, K.; Wang, H.-B.; Li, N.; Wang, J.; Yang, W.-H.; Yin, Z.; Jiao, Z.-G.; Wen, Z.-B.; Li, J.-S. Concentration and Particle Size Distribution of Microbiological Aerosol During Haze Days in Beijing. *Huan Jing Ke Xue* **2015**, *36*, 3144–3149.

19. Elster, J.; D. R.J.; Petit, J.-R.; Reháková, K. Composition of microbiological communities in aerosol, snow and ice samples from remote glaciated areas (Antarctica, Alps, Andes). *Biogeosciences Discuss. Eur. Geosci. Union* **2007**.

20. Brodie, E.L.; de Santis, T.Z.; Moberg-Parker, J.P.; Zubietta, I.X.; Piceno, Y.M.; Andersen, G.L. Urban aerosols harbor diverse and dynamic bacterial populations. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 299–304.

21. Aller, J.Y.; Kuznetsova, M.R.; Jahns, C.J.; Kemp, P.F. The sea surface microlayer as a source of viral and bacterial enrichment in marine aerosols. *J. Aerosol. Sci.* **2005**, *36*, 801–812, doi:10.1016/j.jaerosci.2004.10.012.

22. Hughes, K.A. Aerial dispersal and survival of sewage-derived faecal coliforms in Antarctica. *Atmos. Environ.* **2003**, *37*, 3147–3155, doi:10.1016/s1352-2310(03)00207-3.

23. Bru-Adan, V.; Wery, N.; Moletta-Denat, M.; Boiron, P.; Delgenes, J.P.; Godon, J.J. Diversity of bacteria and fungi in aerosols during screening in a green waste composting plant. *Curr. Microbiol.* **2009**, *59*, 326–335, doi:10.1007/s00284-009-9438-3.

24. Gonzalez-Toril, E.; Robert, A.R.; Delmas, J.; Petit, J.; Komarek, J.; Elster, J. Bacterial diversity of autotrophic enriched cultures from remote, glacial Antarctic, Alpine and Andean aerosol, snow and soil samples. *Biogeosciences Eur. Geosci. Union* **2009**, doi:10.5194/bg-6-33-2009.

25. le Goff, O.; Bru-Adan, V.; Bacheley, H.; Godon, J.J.; Wery, N. The microbial signature of aerosols produced during the thermophilic phase of composting. *J. Appl. Microbiol.* **2010**, *108*, 325–340, doi:10.1111/j.1365-2672.2009.04427.x.

26. Gao, J.-F.; Fan, X.-Y.; Li, H.-Y.; Pan, K.-L. Airborne Bacterial Communities of PM2.5 in Beijing-Tianjin-Hebei Megalopolis, China as Revealed By Illumina MiSeq Sequencing: A Case Study. *Aerosol. Air Qual. Res.* **2017**,
Atmosphere 2020, 11, 919

17, 788–798, doi:10.4209/aaqr.2016.02.0087.
27. Busse, H.J.; Denner, E.B.M.; Buczolits, S.; Salkinoja-Salonen, M.; Bennasar, A.; Kampfer, P. Sphingomonas aurantiaca sp nov., Sphingomonas aerolata sp nov and Sphingomonas faeni sp nov., air- and dustborne and Antarctic, orange-pigmented, psychrotolerant bacteria, and emended description of the genus Sphingomonas. Int. J. Syst. Evol. Microbiol. 2003, 53, 1253–1260, doi:10.1099/ijs.0.02461-0.
28. Abed, R.M.; Ramette, A.; Hubner, V.; de Deckker, P.; de Beer, D. Microbial diversity of eolian dust sources from saline lake sediments and biological soil crusts in arid Southern Australia. FEMS Microbiol. Ecol. 2012, 80, 294–304, doi:10.1111/j.1574-6941.2011.01289.x.
29. de Deckker, P.; Abed, R.M.M.; de Beer, D.; Hinrichs, K.-U.; O’Loingsigh, T.; Schefuß, E.; Stuut, J.-B.W.; Tapper, N.J.; van der Kaars, S. Geochemical and microbiological fingerprinting of airborne dust that fell in Canberra, Australia, in October 2002. Geochim. Geophys. Geosystems 2008, 9, doi:10.1029/2008gc002091.
30. Han, Y.; Li, L.; Liu, J.; Zhang, M. Microbial structure and chemical components of aerosols caused by rotating brushes in a wastewater treatment plant. Environ. Sci. Pollut. Res. Int. 2012, 19, 4097–4108, doi:10.1007/s11356-012-0885-1.
31. Gilbert, J.A.; Steele, J.A.; Caporaso, J.G.; Steinbruck, L.; Reeder, J.; Temperton, B.; Huse, S.; McHardy, A.C.; Knight, R.; Joint, L; et al. Defining seasonal marine microbial community dynamics. ISME J. 2012, 6, 298–308, doi:10.1038/ismej.2011.107.
32. Baylor, E.R.; Peters, V.; Baylor, M.B.J.S. Water-to-air transfer of virus. Science 1977, 197, 763–764.
33. Caliz, J.; Triado-Margarit, X.; Camarero, L.; Casamayor, E.O. A long-term survey unveils strong seasonal patterns in the airborne microbiome coupled to general and regional atmospheric circulations. Proc. Natl. Acad. Sci. USA 2018, 115, 12229–12234, doi:10.1073/pnas.1812826115.
34. Genitsaris, S.; Stefanidou, N.; Katsiapi, M.; Kormas, K.A.; Sommer, U.; Moustaka-Gouni, V. Variability of airborne bacteria in an urban Mediterranean area (Thessaloniki, Greece). Atmos. Environ. 2017, 157, 101–110, doi:10.1016/j.atmosenv.2017.03.018.
35. Deguillaume, L.; Charbonnolot, T.; Joly, M.; Vaïtilingom, M.; Parazols, M.; Marinoni, A.; Amato, P.; Delort, A.M.; Vinatier, V.; Flossmann, A. Classification of clouds sampled at the puy de Dôme (France) from 10 yr monitoring: Mean features of their physico-chemical properties. Atmos. Chem. Phys. Discuss. 2013, 13, 1485–1506.
36. Liu, D.; Mariman, R.; Gerlofs-Nijland, M.E.; Boere, J.F.; Folkerts, G.; Cassee, F.R.; Pinelli, E. Microbiome composition of airborne particulate matter from livestock farms and their effect on innate immune receptors and cells. Sci. Total Environ. 2019, 688, 1298–1307, doi:10.1016/j.scitotenv.2019.06.217.
37. Meadow, J.F.; Altrichter, A.E.; Kembel, S.W.; Kline, J.; Mhuireach, G.; Moriyama, M.; Northcutt, D.; O’Connor, T.K.; Womack, A.M.; Brown, G.Z.; et al. Indoor airborne bacterial communities are influenced by ventilation, occupancy, and outdoor air source. Indoor Air 2014, 24, 41–48, doi:10.1111/ina.12047.
38. Prussin, A.J., 2nd; Vikram, A.; Bibby, K.J.; Marr, L.C. Seasonal Dynamics of the Airborne Bacterial Community and Selected Viruses in a Children’s Daycare Center. PloS ONE 2016, 11, e0151004, doi:10.1371/journal.pone.0151004.
39. Karlsson, E.; Johansson, A.M.; Ahlinder, J.; Lundkvist, M.J.; Singh, N.J.; Brodin, T.; Forsman, M.; Stenberg, P. Airborne microbial biodiversity and seasonality in Northern and Southern Sweden. PeerJ 2020, 8, e8424, doi:10.7717/peerj.8424.
40. Robertson, C.E.; Baumgartner, L.K.; Harris, J.K.; Peterson, K.L.; Stevens, M.J.; Frank, D.N.; Pace, N.R. Culture-independent analysis of aerosol microbiology in a metropolitan subway system. Appl. Environ. Microbiol. 2013, 79, 3485–3493, doi:10.1128/AEM.00331-13.
41. Alebouyeh, M. Fatal sepsis by Bacillus circulans in an immunocompromised patient. Iran. J. Microbiol. 2011, 3, 156–158.
42. Logan, N.A.; Old, D.C.; Dick, H.M. Isolation of Bacillus circulans from a wound infection. J. Clin. Pathol. 1985, 38, 838, doi:10.1136/jcp.38.7.838.
43. Alghamdi, M.A.; Shamy, M.; Redal, M.A.; Khoder, M.; Awad, A.H.; Elserougy, S. Microorganisms associated particulate matter: A preliminary study. Sci. Total Environ. 2014, 479, 109–116, doi:10.1016/j.scitotenv.2014.02.006.
44. Shen, D.K.; Noodeh, A.D.; Kazemi, A.; Grillot, R.; Robson, G.; Brugere, J.F. Characterisation and expression of phospholipases B from the opportunistic fungus Aspergillus fumigatus. FEMS Microbiol. Lett. 2004, 239, 87–93, doi:10.1016/j.femsle.2004.08.019.
45. Zuraimi, M.S.; Fang, L.; Tan, T.K.; Chew, F.T.; Tham, K.W. Airborne fungi in low and high allergic
prevalence child care centers. Atmos. Environ. 2009, 43, 2391–2400, doi:10.1016/j.atmosenviron.2009.02.004.

46. Du, P.; Du, R.; Ren, W.; Lu, Z.; Fu, P. Seasonal variation characteristic of inhalable microbial communities in PM2.5 in Beijing city, China. Sci. Total Environ. 2018, 610, 308–315, doi:10.1016/j.scitotenv.2017.07.097.

47. Yan, D.; Zhang, T.; Su, J.; Zhao, L.-L.; Wang, H.; Fang, X.-M.; Zhang, Y.-Q.; Liu, H.-Y.; Yu, L.-Y.; Schaffner, D.W. Structural Variation in the Bacterial Community Associated with Airborne Particulate Matter in Beijing, China, during Hazy and Nonhazy Days. Appl. Environ. Microbiol. 2018, 84, doi:10.1128/aem.00004-18.

48. Park, J.; Ichijo, T.; Nasu, M.; Yamaguchi, N. Investigation of bacterial effects of Asian dust events through comparison with seasonal variability in outdoor airborne bacterial community. Sci. Rep. 2016, 6, 35706, doi:10.1038/srep35706.

49. Nishimura, Y.; Kenzaka, T.; Sueyoshi, A.; Li, P.; Fujiyama, H.; Baba, T.; Yamaguchi, N.; Nasu, M. Similarity of bacterial community structure between Asian dust and its sources determined by rRNA gene-targeted approaches. Microbes Environ. 2010, 25, 22–27, doi:10.1264/jsme2.me09166.

50. Cha, S.; Lee, D.; Jang, J.H.; Lim, S.; Yang, D.; Seo, T. Alterations in the airborne bacterial community during Asian dust events occurring between February and March 2015 in South Korea. Sci. Rep. 2016, 6, 37271, doi:10.1038/srep37271.

51. Li, Y.; Lu, R.; Li, W.; Xie, Z.; Song, Y. Concentrations and size distributions of viable bioaerosols under various weather conditions in a typical semi-arid city of Northwest China. J. Aerosol. Sci. 2017, 106, 83–92, doi:10.1016/j.jaerosci.2017.01.007.

52. Yao, Z.X.M. Monitoring of bioaerosol inhalation risks in different environments using a six-stage Andersen sampler and the PCR-DGGE method. Environ. Monit. Assess. 2013, doi:10.1007/s10661-012-2844-1.

53. Gao, M.; Qiu, T.; Jia, R.; Han, M.; Song, Y.; Wang, X. Concentration and size distribution of viable bioaerosols during non-haze and haze days in Beijing. Environ. Sci. Pollut. Res. Int. 2015, 22, 4359–4368, doi:10.1007/s11356-014-3675-0.

54. Dong, L.; Qi, J.; Shao, C.; Zhong, X.; Gao, D.; Cao, W.; Gao, J.; Bai, R.; Long, G.; Chu, C. Concentration and size distribution of total airborne microbes in hazy and foggy weather. Sci. Total Environ. 2016, 541, 1011–1018, doi:10.1016/j.scitotenv.2015.10.001.

55. Fang, Z.; Ouyang, Z.; Zheng, H.; Wang, X. Concentration and Size Distribution of Culturable Airborne Microorganisms in Outdoor Environments in Beijing, China. Aerosol. Sci. Technol. 2008, 42, 325–334, doi:10.1080/02786800802068657.

56. Li, M.; Qi, J.; Zhang, H.; Huang, S.; Li, L.; Gao, D. Concentration and size distribution of bioaerosols in an outdoor environment in the Qingdao coastal region. Sci. Total Environ. 2011, 409, 3812–3819, doi:10.1016/j.scitotenv.2011.06.001.

57. Fahlgren, C.; Bratbak, G.; Sandaa, R.-A.; Thyrrhaug, R.; Zweifel, U.L. Diversity of airborne bacteria in samples collected using different devices for aerosol collection. Aerobiologia 2010, 27, 107–120, doi:10.1007/s10453-010-9181-z.

58. Zhong, S.; Zhang, L.; Jiang, X.; Gao, P. Comparison of chemical composition and airborne bacterial community structure in PM2.5 during haze and non-haze days in the winter in Guilin, China. Sci. Total Environ. 2019, 655, 202–210, doi:10.1016/j.scitotenv.2018.11.268.

59. Xie, Z.; Li, Y.; Lu, R.; Li, W.; Fan, C.; Liu, P.; Wang, J.; Wang, W. Characteristics of total airborne microbes at various air quality levels. J. Aerosol. Sci. 2018, 116, 57–65, doi:10.1016/j.jaerosci.2017.11.001.

60. Bandowe, B.A.; Meusel, H.; Huang, R.J.; Ho, K.; Cao, J.; Hoffmann, T.; Wilcke, W. PM(2.5)-(5)-bound oxygenated PAHs, nitro-PAHs and parent-PAHs from the atmosphere of a Chinese megacity: Seasonal variation, sources and cancer risk assessment. Sci. Total Environ. 2014, 473, 77–87, doi:10.1016/j.scitotenv.2013.11.108.

61. Zhang, Q.; Shen, Z.; Cao, J.; Zhang, R.; Zhang, L.; Huang, R.J.; Zheng, C.; Wang, L.; Liu, S.; Xu, H.; et al. Variations in PM2.5, TSP, BC, and trace gases (NOx, SO2, and O3) between haze and non-haze episodes in winter over Xi’an, China. Atmos. Environ. 2015, 112, 64–71, doi:10.1016/j.atmosenv.2015.04.033.

62. Wei, K.; Zou, Z.; Zheng, Y.; Li, J.; Shen, F.; Wu, C.Y.; Wu, Y.; Hu, M.; Yao, M. Ambient bioaerosol particle dynamics observed during haze and sunny days in Beijing. Sci. Total Environ. 2016, 550, 751–759, doi:10.1016/j.scitotenv.2016.01.137.

63. Yamamoto, N.; Bibby, K.; Qian, J.; Hospodsky, D.; Rismani-Yazdi, H.; Nazaroff, W.W.; Peccia, J. Particle-size distributions and seasonal diversity of allergenic and pathogenic fungi in outdoor air. ISME J 2012, 6, 1801–1811, doi:10.1038/ismej.2012.30.
64. Sykes, P.; Jones, K.; Wildsmith, J.D. Managing the potential public health risks from bioaerosol liberation at commercial composting sites in the UK: An analysis of the evidence base. *Resour. Conserv. Recycl.* 2007, 52, 410–424, doi:10.1016/j.resconrec.2007.05.005.

65. Ye, L.; Zhang, T. Pathogenic bacteria in sewage treatment plants as revealed by 454 pyrosequencing. *Environ. Sci. Technol.* 2011, 45, 7172–7179, doi:10.1021/es101045e.

66. Perry, A.; Lambert, P. Propionibacterium acnes: Infection beyond the skin. *Expert Rev. Anti-Infect. Ther.* 2011, 9, 1149–1156, doi:10.1586/eri.11.137.

67. Antunes, L.C.; Visca, P.; Towner, K.J. Acinetobacter baumannii: Evolution of a global pathogen. *Pathog. Dis.* 2014, 71, 292–301, doi:10.1111/2049-632X.12125.

68. Schaberg, D.R.; Culver, D.H.; Gaynes, R.P. Major trends in the microbial etiology of nosocomial infection. *Am. J. Med.* 1991, 91, S72–S75, doi:10.1016/0002-9343(91)90346-Y.

69. Morot-Bizot, S.C.; Talon, R.; Leroy, S. Development of a multiplex PCR for the identification of Staphylococcus genus and four staphylococcal species isolated from food. *J. Appl. Microbiol.* 2004, 97, 1087–1094, doi:10.1111/j.1365-2672.2004.02399.x.

70. Schönfeld, J.; Gelsomino, A.; van Overbeek, L.S.; Gorissen, A.; Smalla, K.; van Elsas, J.D. Effects of compost addition and simulated solarisation on the fate ofRalstonia solanacearum biovar 2 and indigenous bacteria in soil. *FEMS Microbiol. Ecol.* 2003, 43, 63–74.

71. Innocente, E.; Squizzato, S.; Visin, F.; Facca, C.; Rampazzo, G.; Bertolini, V.; Gandolfi, I.; Franzetti, A.; Ambrosini, R.; Bestetti, G. Influence of seasonality, air mass origin and particulate matter chemical composition on airborne bacterial community structure in the Po Valley, Italy. *Sci. Total Environ.* 2017, 593–594, 677-687, doi:10.1016/j.scitotenv.2017.03.199.

72. Albrecth, A.; Fischer, G.; Brunnemann-Stubbe, G.; Jackel, U.; Kampfer, P. Recommendations for study design and sampling strategies for airborne microorganisms, MVOG and odours in the surrounding of composting facilities. *Int. J. Hyg. Environ. Health* 2008, 211, 121–131, doi:10.1016/j.ijheh.2007.05.004.

73. Ibrahim, A.S.; Spellberg, B.; Walsh, T.J.; Kontoyiannis, D.P. Pathogenesis of mucormycosis. *Clin. Infect. Dis.* 2012, 54, S16–S22.

74. Madsen, A.M.; Zervas, A.; Tendal, K.; Nielsen, J.L. Microbial diversity in bioaerosol samples causing ODTS compared to reference bioaerosol samples as measured using Illumina sequencing and MALDI-TOF. *Environ. Res.* 2015, 140, 255–267, doi:10.1016/j.envres.2015.03.027.

75. Liu, B.; Ichinose, T.; He, M.; Kobayashi, F.; Maki, T.; Yoshida, S.; Yoshida, Y.; Arashidani, K.; Takano, H.; Nishikawa, M. Lung inflammation by fungus, Bjerkandera adusta isolated from Asian sand dust (ASD) aerosol and enhancement of ovalbumin-induced lung eosinophilia by ASD and the fungus in mice. *Allergy Asthma Clin. Immunol.* 2014, 10, 10.

76. Heyrman, J.; Balcaen, A.; Rodriguez-Diaz, M.; Logan, N.A.; Swings, J.; de Vos, P. Bacillus decolorationis sp. nov., isolated from biodeteriorated parts of the mural paintings at the Servilia tomb (Roman necropolis of Carmona, Spain) and the Saint-Catherine chapel (Castle Herberstein, Austria). *Int. J. Syst. Evol. Microbiol.* 2003, 53, 499-463, doi:10.1099/ijs.0.02452-0.

77. Douwes, J.; Thorne, P.; Pearce, N.; Heederik, D. Bioaerosol health effects and exposure assessment: Progress and prospects. *Ann. Occup. Hyg.* 2003, 47, 187–200, doi:10.1093/annhyg/meg032.

78. Herr, C.E.W.; Zur-Nieden, A.; Jankowski, M.; Stilianakis, N.I.; Boedeker, R.H.; Eikmann, T.F. Effects of bioaerosol polluted outdoor air on airways of residents: A cross sectional study. *Occup. Environ. Med.* 2003, 60, 336–342.

79. Borlée, F.; Yzermans, C.J.; Aalders, B.; Rooijackers, J.; Krop, E.; Maassen, C.B.M.; Schellevis, F.; Brunekreef, B.; Heederik, D.; Smit, L.A.M. Air pollution from livestock farms is associated with airway obstruction in neighboring residents. *Am. J. Respir. Crit. Care Med.* 2017, 196, 1152–1161.

80. McClendon, C.J.; Gerald, C.L.; Waterman, J.T. Farm animal models of organic dust exposure and toxicity: Insights and implications for respiratory health. *Curr. Opin. Allergy Clin. Immunol.* 2015, 15, 137–144, doi:10.1097/ACI.0000000000000143.

81. Radon, K.; Schulze, A.; Ehrenstein, V.; van Strien, R.T.; Praml, G.; Nowak, D. Environmental exposure to confined animal feeding operations and respiratory health of neighboring residents. *Epidemiology* 2007, 18, 300–308, doi:10.1097/01.ede.0000259966.62137.84.

82. Cambra-Lopez, M.; Aarmin, A.J.; Zhao, Y.; Calvet, S.; Torres, A.G. Airborne particulate matter from livestock production systems: A review of an air pollution problem. *Environ. Pollut.* 2010, 158, 1–17, doi:10.1016/j.envpol.2009.07.011.
83. Madsen, A.M.; Tendal, K.; Schlunssen, V.; Helberg, I. Organic dust toxic syndrome at a grass seed plant caused by exposure to high concentrations of bioaerosols. *Ann. Occup. Hyg.* 2012, 56, 776–788, doi:10.1093/annhyg/mes012.

84. Pratt, K.A.; de Mott, P.J.; French, J.R.; Wang, Z.; Westphal, D.L.; Heymsfield, A.J.; Twomey, C.H.; Prenni, A.J.; Prather, K.A. In situ detection of biological particles in cloud ice-crystals. *Nat. Geosci.* 2009, 2, 398–401.

85. Posch, U.; Martin, S.T.; Sinha, B.; Chen, Q.; Gunthe, S.S.; Huffman, J.A.; Borrán, S.; Farmer, D.K.; Garland, R.M.; Helas, G.; et al. Rainforest aerosols as biogenic nuclei of clouds and precipitation in the Amazon. *Science* 2010, 329, 1513–1516, doi:10.1126/science.1191056.

86. Qi, J.H.; Gao, H.W. Environment and climate effect of bioaerosol: A review. *Ecol. Environ.* 2006, 15, 854–861.

87. Deguillaume, L.; Leriche, M.; Amato, P.; Ariya, P.A.; Delort, A.M.; Posch, U.; Chaumerliac, N.; Bauer, H.; Flossmann, A.; Morris, C.E. Microbiology and atmospheric processes: Chemical interactions of primary biological aerosols. *Biogeosciences* 2008, 5, 1073–1084.

88. Möhler, O.; de Mott, P.J.; Vali, G.; Levin, Z. Microbiology and atmospheric processes: The role of biological particles in cloud physics. *Biogeosciences* 2007, 4, doi:10.5194/bg-4-2559-2007.

89. Després, V.; Huffman, J.A.; Burrows, S.M.; Hoose, C.; Safarov, A.; Buryak, G.; Fröhlich-Nowoisky, J.; Elbert, W.; Andreade, M.; Pöschl, U.; et al. Primary biological aerosol particles in the atmosphere: A review. *Tellus B Chem. Phys. Meteorol.* 2012, 64, doi:10.3402/tellusb.v64i0.15598.

90. Murray, B.J.; O’Sullivan, D.; Atkinson, J.D.; Webb, M.E. Ice nucleation by particles immersed in supercooled cloud droplets. *Chem. Soc. Rev.* 2012, 41, 6519–6554, doi:10.1039/c2cs35200a.

91. Morris, C.E.; Georgakopoulos, D.G.; Sands, D.C. Ice nucleation active bacteria and their potential role in precipitation. *J. Phys.* 2004, 121, 87–103, doi:10.1051/jp4:2004121004.

92. Fröhlich-Nowoisky, J.; Hill, T.C.J.; Pummer, B.G.; Yordanova, P.; Franc, G.D.; Pöschl, U. Ice nucleation activity in the widespread soil fungus Mortierella alpina. *Biogeosciences* 2015, 12, 1057–1071, doi:10.5194/bg-12-1057-2015.

93. Kieft, T.L.; Ruscelii, T. Characterization of biological ice nuclei from a lichen. *J. Bacteriol.* 1990, 172, 3519–3523, doi:10.1128/jb.172.6.3519-3523.1990.

94. Pouler, S.; Richard, C.; Martin, J.-G.; Antoun, H. Ice nucleation activity in Fusarium acuminatum and Fusarium avenaceum. *Appl. Environ. Microbiol.* 1992, 58, 2960–2964.

95. Pummer, B.G.; Bauer, H.; Bernardi, J.; Piechule, S.; Grothe, H. Suspendsable macromolecules are responsible for ice nucleation activity of birch and conifer pollen. *Atmos. Chem. Phys.* 2012, 12, 2541–2550, doi:10.5194/acp-12-2541-2012.

96. Gao, M.; Yan, X.; Qiu, T.; Han, M.; Wang, X. Variation of correlations between factors and culturable airborne bacteria and fungi. *Atmos. Environ.* 2016, 128, 10–19, doi:10.1016/j.atmosenv.2015.12.008.

97. Haas, D.; Galler, H.; Luxner, J.; Zarfel, G.; Buzina, W.; Friedl, H.; Marth, E.; Habib, J.; Reithaller, F.F. The concentrations of culturable microorganisms in relation to particulate matter in urban air. *Atmos. Environ.* 2013, 65, 215–222, doi:10.1016/j.atmosenv.2012.10.031.

98. Ulevicius, V.; Peciulyte, D.; Mordas, G.; Lugauskas, A. Field study on changes in viability of airborne fungal propagules exposed to solar radiation. *J. Aerosol. Sci.* 2000, 31, 5961–5962.

99. Joly, M.; Amato, P.; Sancelme, M.; Vinatier, V.; Abrantes, M.; Deguillaume, L.; Delort, A.-M. Survival of microbial isolates from clouds toward simulated atmospheric stress factors. *Atmos. Environ.* 2015, 117, 92–98, doi:10.1016/j.atmosenv.2015.07.009.

100. Hwang, S.H.; Park, J.B. Comparison of culturable airborne bacteria and related environmental factors at underground subway stations between 2006 and 2013. *Atmos. Environ.* 2014, 84, 289–293, doi:10.1016/j.atmosenv.2013.11.064.

101. Ho, H.-M.; Rao, C.Y.; Hsu, H.-H.; Chiu, Y.-H.; Liu, C.-M.; Chao, H.J. Characteristics and determinants of ambient fungal spores in Hualien, Taiwan. *Atmos. Environ.* 2005, 39, 5839–5850, doi:10.1016/j.atmosenv.2005.06.034.

102. Liang, L.; Engling, G.; Cheng, Y.; Duan, F.; Du, Z.; He, K. Rapid detection and quantification of fungal spores in the urban atmosphere by flow cytometry. *J. Aerosol. Sci.* 2013, 66, 179–186, doi:10.1016/j.jaerosci.2013.08.013.

103. Bowers, R.M.; McCubbin, I.B.; Hallar, A.G.; Fierer, N. Seasonal variability in airborne bacterial communities at a high-elevation site. *Atmos. Environ.* 2012, 50, 41–49, doi:10.1016/j.atmosenv.2012.01.005.

104. Hjelmroos, M. Relationship between airborne fungal spore presence and weather variables: Cladosporium and Alternaria. *Grana* 1993, 32, 40–47, doi:10.1080/00173139309436418
105. Maki, T.; Hara, K.; Kobayashi, F.; Kurotsuki, Y.; Kakikawa, M.; Matsuki, A.; Chen, B.; Shi, G.; Hasegawa, H.; Iwasaka, Y. Vertical distribution of airborne bacterial communities in an Asian-dust downwind area, Noto Peninsula. Atmos. Environ. 2015, 119, 282–293, doi:10.1016/j.atmosenv.2015.08.052.

106. Maki, T.; Kurotsuki, Y.; Orishi, K.; Lee, K.C.; Pointing, S.B.; Jugder, D.; Yamanaka, N.; Hasegawa, H.; Shinoda, M. Variations in the structure of airborne bacterial communities in Tsgot-Ovoo of Gobi desert area during dust events. Air Qual. Atmos Health 2017, 10, 249–260, doi:10.1007/s11869-016-0430-3.

107. Rodo, X.; Ballester, J.; Cayan, D.; Melish, M.E.; Nakamura, Y.; Uehara, R.; Burns, J.C. Association of Kawasaki disease with tropospheric wind patterns. Sci. Rep. 2011, 1, 152, doi:10.1038/srep00152.

108. Yang, Y.J.; Itoh, T.; Yokobori, S.; Shimada, H.; Itahashi, S.; Satoh, K.; Ohba, H.; Narumi, I.; Yamagishi, A. Deinococcus aetherius sp nov., isolated from the stratosphere. Int. J. Syst. Evol. Microbiol. 2010, 60, 776–779, doi:10.1099/ijs.0.010876-0.

109. Griffin, D.W. Non-spore forming eubacteria isolated at an altitude of 20,000 m in Earth’s atmosphere: Extended incubation periods needed for culture-based assays. Aerobiologia 2008, 24, 19–25, doi:10.1007/s10433-007-9078-7.

110. das Sarma, P.; DasSarma, S. Survival of microbes in Earth’s stratosphere. Curr. Opin. Microbiol. 2018, 43, 24–30, doi:10.1016/j.mib.2017.11.002.

111. Dehel, T.; Lorge, F.; Dickinson, M. Uplift of microorganisms by electric fields above thunderstorms. J. Electrost. 2008, 66, 463–466, doi:10.1016/j.jelestat.2008.04.014.

112. Mainelis, G.; Willeke, K.; Baron, P.; Grinshpun, S.A.; Reponen, T. Induction Charging and Electrostatic Classification of Micrometer-Size Particles for Investigating the Electrobiological Properties of Airborne Microorganisms. Aerosol. Sci. Technol. 2010, 36, 479–491, doi:10.1080/027868202753571304.

113. Heo, K.J.; Kim, H.B.; Lee, B.U. Concentration of environmental fungal and bacterial bioaerosols during the monsoon season. J. Aerosol. Sci. 2014, 77, 31–37, doi:10.1016/j.jaerosci.2014.07.001.

114. Salonen, H.; Duchaine, C.; Mazaheri, M.; Clifford, S.; Morawska, L. Airborne culturable fungi in naturally ventilated primary school environments in a subtropical climate. Atmos. Environ. 2015, 106, 412–418, doi:10.1016/j.atmosenv.2014.07.052.

115. Gao, M.; Jia, R.; Qiu, T.; Han, M.; Song, Y.; Wang, X. Seasonal size distribution of airborne culturable bacteria and fungi and preliminary estimation of their deposition in human lungs during non-haze and haze days. Atmos. Environ. 2015, 118, 203–210, doi:10.1016/j.atmosenv.2015.08.004.

116. Lee, T.; Grinshpun, S.A.; Martuzevicius, D.; Adhikari, A.; Crawford, C.M.; Reponen, T. Culturability and concentration of indoor and outdoor airborne fungi in six single-family homes. Atmos. Environ. 2006, 40, 2902–2910, doi:10.1016/j.atmosenv.2006.01.011.

117. Hurtado, L.; Rodríguez, G.; López, J.; Castillo, J.E.; Molina, L.; Zavala, M.; Quintana, P.J.E. Characterization of atmospheric bioaerosols at 9 sites in Tijuana, Mexico. Atmos. Environ. 2014, 96, 430–436, doi:10.1016/j.atmosenv.2014.07.018.

118. Winter, C.; Bouvier, T.; Weinbauer, M.G.; Thingstad, T.F. Trade-offs between competition and defense specialists among unicellular planktonic organisms: The “killing the winner” hypothesis revisited. Microbiol Mol. Biol. Rev. 2010, 74, 42–57, doi:10.1128/MMBR.00034-09.

119. Yamaguchi, N.; Park, J.; Kodama, M.; Ichijo, T.; Baba, T.; Nasu, M. Changes in the airborne bacterial community in outdoor environments following Asian dust events. Microbes Environ. 2014, 29, 82–88, doi:10.1264/jsme2.me13080.