Environment International 145 (2020) 106156

Contents lists available at ScienceDirect

Environment International

journal homepage: www.elsevier.com/locate/envint

Review article

Airborne bacterial communities of outdoor environments and their associated influencing factors

Tay Ruiz-Gil [a,b], Jacquelinne J. Acuña [b,c,e], So Fujiyoshi [b,c,d,e], Daisuke Tanaka [f], Jun Noda [e,g], Fumito Maruyama [b,c,d,e], Milko A. Jorquera [b,c,e,*]

[a] Doctorado en Ciencias de Recursos Naturales, Facultad de Ingeniería y Ciencias, Universidad de La Frontera, Temuco, Chile
[b] Laboratorio de Ecología Microbiana Aplicada (EMALAB), Departamento de Ciencias Químicas y Recursos Naturales, Universidad de La Frontera, Temuco, Chile
[c] Network for Extreme Environment Research (NEXER), Scientific and Technological Bioresource Nucleus (BIOREN), Universidad de La Frontera, Temuco, Chile
[d] Microbial Genomics and Ecology, Office of Industry-Academia-Government and Community Collaboration, Hiroshima University, Hiroshima, Japan
[e] Center for Holobiome and Built Environment (CHOBE), Hiroshima University, Japan
[f] Graduate School of Science and Engineering, University of Toyama, Toyama, Japan
[g] Graduate School of Veterinary Science, Rakuno Gakuen University, Hokkaido, Japan

ARTICLE INFO

Handling Editor: Xavier Querol

Keywords:
Airborne bacteria
Atmosphere
Bacterial communities
Bioaerosols
Outdoor environments

ABSTRACT

Microbial entities (such bacteria, fungi, archaea and viruses) within outdoor aerosols have been scarcely studied compared with indoor aerosols and nonbiological components, and only during the last few decades have their studies increased. Bacteria represent an important part of the microbial abundance and diversity in a wide variety of rural and urban outdoor bioaerosols. Currently, airborne bacterial communities are mainly sampled in two aerosol size fractions (2.5 and 10 μm) and characterized by culture-dependent (plate-counting) and culture-independent (DNA sequencing) approaches. Studies have revealed a large diversity of bacteria in bioaerosols, highlighting Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes as ubiquitous phyla. Seasonal variations in and dispersion of bacterial communities have also been observed between geographical locations as has their correlation with specific atmospheric factors. Several investigations have also suggested the relevance of airborne bacteria in the public health and agriculture sectors as well as remediation and atmospheric processes. However, although factors influencing airborne bacterial communities and standardized procedures for their assessment have recently been proposed, the use of bacterial taxa as microbial indicators of specific bioaerosol sources and seasonality have not been broadly explored. Thus, in this review, we summarize and discuss recent advances in the study of airborne bacterial communities in outdoor environments and the possible factors influencing their abundance, diversity, and seasonal variation. Furthermore, airborne bacterial activity and bioprospecting in different fields (*e.g.*, the textile industry, the food industry, medicine, and bioremediation) are discussed. We expect that this review will reveal the relevance and influencing factors of airborne bacteria in outdoor environments as well as stimulate new investigations on the atmospheric microbiome, particularly in areas where air quality is a public concern.

1. Introduction

Aerosols are defined as suspended particles in the air, with 'bioaerosols' being those with a biological origin. Nonbiological aerosols (*e.g.*, dust, ash, heavy metals, sulfur oxides and organic compounds) have been extensively studied due to their negative effects on public health and natural ecosystems (Camatini et al., 2017; Grennfelt et al., 2019; Tang et al., 2018; Tomasi et al., 2017). Despite the inherent limitations that online search engines possess due to the high number of homologous words when using limited terms as keywords, as illustration, we carried out a search on the Web of Science database (Fig. 1) based on the keywords "aerosol" and "bioaerosol", and we determined the number of studies that used the terms "outdoor" and "indoor" over the years. While aerosols have been studied during the last one hundred years, reaching approximately 7,000 published articles to date, bioaerosols have 30 years of research and approximately 240 articles published to date. At the global level, bioaerosols represent a quarter of the aerosol mass (Després et al., 2012), and several investigations have

* Corresponding author at: Departamento de Ciencias Químicas y Recursos Naturales, Universidad de La Frontera, Ave. Francisco Salazar 01145, Temuco, Chile.
E-mail address: milko.jorquera@ufrontera.cl (M.A. Jorquera).

https://doi.org/10.1016/j.envint.2020.106156
Received 26 May 2020; Received in revised form 20 September 2020; Accepted 21 September 2020
Available online 8 October 2020

revealed their prominent roles in climate, ecosystem health and atmospheric processes (Morris et al., 2014; Fröhlich-Nowoisky et al., 2016). However, most bioaerosol studies have concentrated on indoor environments (Gao et al., 2015; Fujiyoshi et al., 2017; Kim et al., 2018). As shown in Fig. 1, despite an increase in aerosol and bioaerosol studies during recent years, research on bioaerosols in outdoor environments accounts for the lowest proportion of studies.

Within bioaerosols, we mainly find isolated or associated microbial entities (bacteria, fungi, protozoa, algae, archaea and viruses), solid fragments or excretions of organisms, plant debris, leaf litter and pollen. Anthropogenic activities (*e.g.*, farming and waste treatment plants) and natural processes (*e.g.*, sea spray, pollination, volcanic eruption, wildfires and desert dust) have been described as principal emission sources of bioaerosols into the atmosphere (Tomasi et al., 2017; Després et al., 2012). Similarly, concentrations and dispersion ranges are determined by physicochemical (*e.g.*, particulate matter size and concentration) and meteorological (*e.g.*, wind speed, relative humidity, temperature and solar radiation) conditions (Bertolini et al., 2013; Zhen et al., 2017). Since biological components can exist from <0.1 μm for viruses, 1 to 10 μm for bacteria, vegetative cells, and spores, and up to 100 μm for plant pollens, they distribute in a wide range of particle sizes. Moreover, those biological components may agglomerate by themselves and/or attach to abiotic particles in the air. The atmosphere is categorized as an extreme environment where nonbiological aerosol particles can serve as refuges and energy sources for airborne microorganisms; the abundance and diversity of airborne microorganisms are highly influenced by the type of suspended nonbiological particles and their sizes (Bowers et al., 2013; Cao et al., 2014; Fujiyoshi et al., 2017; Tanaka et al., 2020). High airborne microbial concentrations, from 10^3 to 10^7 cells m^{-3} of air (Gandolfi et al., 2013; Maki et al., 2017), can be found from mountain peaks to desert dust clouds. Some metagenomics studies have also reported notable relative abundances of bacterial reads in aerosols samples (Bowers et al., 2013; Cao et al., 2014).

In general terms, human airborne bacterial pathogens and human-associated airborne bacteria have been widely studied (Fröhlich-Nowoisky et al., 2016; Kim et al., 2018; Griffin et al., 2017; Polymenakou, 2012), and their infection and transmission mechanisms have recently been reviewed by Meena et al. (2019). However, airborne bacteria in outdoor environments have relevance not only to public health but also to agriculture, given the dispersion and deposition of phytopathogens on leaves and stem surfaces (Monteil et al., 2014; Cevallos-Cevallos et al., 2012). In addition, the ice nucleation activity of airborne bacteria (most of which are reported as phytopathogens) may induce ice and cloud formation, which promotes precipitation, altering the climate and microbial biogeographical dispersion (Bigg et al., 2015; Christner et al., 2008). Studies have also revealed that airborne bacterial composition and dispersion in the atmosphere can be influenced by specific micro- and macroscale determinants, such as land use, emission sources, concentration and particle size, air humidity, wind speed, and temperature (Fujiyoshi et al., 2017; Bowers et al., 2011; Gandolfi et al., 2015; Šantl-Temkiv et al., 2018).

A recent review of airborne bacterial communities has described factors influencing bacterial concentrations and communities in built environments, proposing the establishment of a standard procedure for the study of indoor airborne bacteria using four factors (temperature, relative humidity, air exchange rate, and occupant density) (Fujiyoshi et al., 2017). However, atmospheric factors regulating airborne bacterial communities in outdoor environments at the local and global levels as well as bacterial taxa that can serve as microbial indicators of specific bioaerosol sources and seasonality need to be demonstrated in both urban and rural environments. In this review, we provide a current overview of the advances in the study of airborne bacterial communities in outdoor environments and the possible factors influencing their abundance, diversity and seasonal variation in diverse outdoor environments. In addition, the activity and potential biotechnological applications of airborne bacteria are discussed.

2. Study of airborne bacterial communities

Traditionally, bacterial communities in bioaerosols have been studied using culture-based methods, but it is widely known that culture media capture only a small fraction of the total environmental bacteria, and the same trend has been observed for bioaerosols (Gandolfi et al., 2013; Duquenne, 2018). DNA-based methods are currently used to understand total airborne bacterial communities, providing rapid, sensitive, and specific information to overcome the limitations mentioned above (Peccia and Hernandez, 2006). However, methods for aerosol sampling are very dissimilar, and the development of standardized protocols for the study of bioaerosols is still in early stages (Ferguson et al., 2019). In addition, bioaerosol biomass and the concentration of microbial genetic material are generally low, and the resulting yields depend on the collection device, sample matrix, duration and airflow

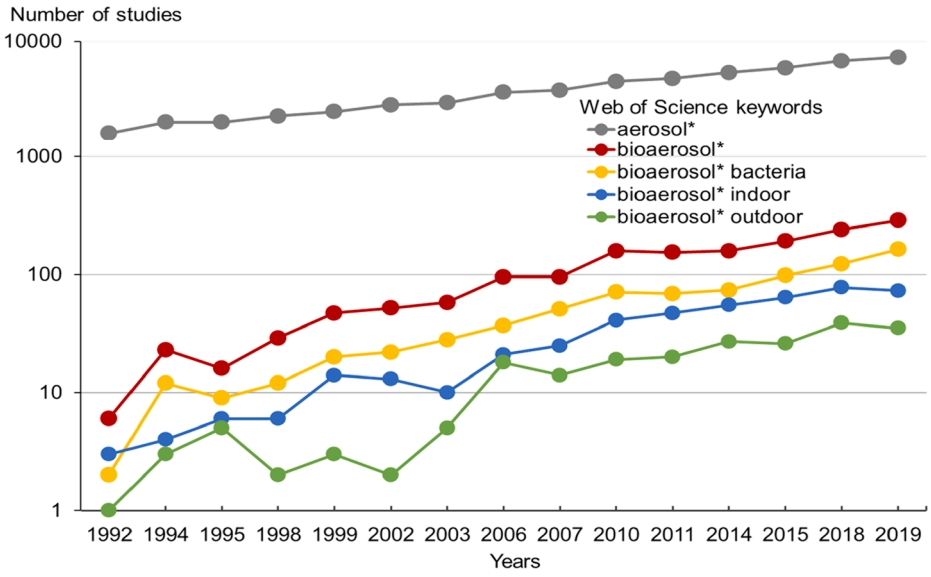

Fig. 1. Number of published studies per year (until 2019) on aerosols, bioaerosols and specific subjects, such as bioaerosol bacteria and bioaerosols in indoor and outdoor environments. The results are based on the Web of Science (WoS; www.webofknowledge.com) database. The asterisks are used for the inclusion of singular and plural forms of keywords in the WoS search engine. The search was updated on July 16th, 2020.

rate; therefore, the sampling method used is crucial for the study of airborne bacteria in outdoor environments (Luhung et al., 2015). Finally, it is necessary to mention that after sampling, the efficiency of nucleic acid extraction and the purity of the nucleic acids obtained need to be improved. Because inhibitors can frequently be present in high concentrations in aerosol samples, they affect molecular biology methods, such as the amplification of specific DNA fragments by polymerase chain reaction (PCR) (Ferguson et al., 2019).

2.1. Methods used for bioaerosol sampling

Currently, there is a wide variety of methods used for bioaerosol sampling, and each method presents both advantages and disadvantages. The methods can be divided into four main categories, namely, gravity, impaction, liquid impingement and filtration, and their selection depends on the objective of the study and the subsequent analysis (Gandolfi et al., 2013).

Bioaerosol settlement onto an agar medium by gravity is the least expensive and simplest method; therefore, it has extensively been used in air microbiology. Classic examples are the collection of rain, hail and snow with a subsequent cultivation step. However, the gravity method is biased by the weight of the particles, wind (direction and speed) and the bacterial concentration, which cannot be calculated because the air volume sampled is unknown. In the other three methods (impaction, liquid impingement and filtration), air-forced samplers are used, allowing determination of the concentration of bacterial cells and particle size analyses. However, the disadvantages of these methods are cellular stress caused by viability losses and a decrease in retrieval efficiency due to particle bounce and flow rates, which are often low (Griffin, 2007). Impingers use a bubbling or whirlwind of liquid for bioaerosol collection. The main advantages of this approach are the lack of desiccation problems, options for sample dilution or concentration, and varied posterior analysis by both culture-dependent and culture-independent methods, such as cultivation or molecular, microscopy and flow cytometry approaches. However, collection time and low efficiencies for fine particle ($<$2.5 μm) collection can influence their analysis (Ferguson et al., 2019). The filtration method, in which air is forced through a porous membrane, is usually highly efficient for fine particle collection, simple, and inexpensive; this method is generally used in culture-independent analyses (Griffin et al., 2017). However, DNA collection and extraction efficiencies depend on the membrane material used (fibrous (*e.g.*, glass fiber and cellulose), membranous (*e.g.*, gelatin and polyvinyl chloride), or flat (*e.g.*, polycarbonate) and storage conditions (Duquenne, 2018).

2.2. Characterization methods

The first methods used in outdoor aerobiological studies were based on cultivation, in which Gram-positive bacteria are generally dominant, probably due to their spore-forming characteristics and resistance to desiccation and radiation (Griffin et al., 2017). Several studies have reported concentrations of bioaerosols up to 1000 times lower by cultivation than those measured by culture-independent methods, such as PCR (Duquenne, 2018). Although other modern characterization techniques have reported overlapping findings, the results are usually substantially different (Ravva et al. 2012; Fahlgren et al. 2010), and culturable bacteria represent only 1 to 20% of the total bacterial diversity (Temkiv et al. 2012; Vaïtilingom et al. 2012). However, using the sequences and taxonomic affiliations of airborne bacteria, a recent study estimated that 50%–80% of airborne bacterial taxa had closely related cultured bacteria and hence, could be cultured (Martiny, 2019). Despite disadvantages, cultivation remains the method of choice for obtaining reliable information on the metabolism and physiology of airborne bacterial strains. For example, pigmentation, which protects cells from UV irradiation and contributes to survival at low temperatures, was revealed as a very common feature among cultured airborne bacteria (Cho and Hwang, 2011; Vaïtilingom et al. 2012). Pathogenic traits or antibiotic-resistant strains from aerosols can also be determined by epidemiological and sanitary surveys, depending on the culturability and viability of bacterial cells (Gandolfi et al., 2013). However, bacteria may lose their culturability after atmospheric exposure and/or during sampling and cultivation as described by Cevallos-Cevallos et al. (2012).

Currently, culture-independent molecular techniques are also widely used in aeromicrobiology. The staining of microbial cells with fluorescent dyes and subsequent fluorescence microscopy observations allow the quantification and recognition of viable cells; however, low cell concentrations or bacterial activity may impede these studies (Bowers et al., 2011). In this context, PCR-based methods have made it possible to study outdoor environments and eliminated the impediment caused by the small fraction of culturable cells or low concentrations of bacteria. Compared to cultivation methods, a greater variety of samplers, which have the highest sensitivity, speed and independence from viability, can be used for the collection of bacteria. As a result, it has been shown that the diversity of the bacterial community in the air from outdoor environments apparently approximates that observed in studies done in terrestrial or aquatic environments (Gandolfi et al., 2013; Smets et al., 2016). In addition, through the quantification and identification of nucleic acid (DNA and RNA) markers, both the abundance and diversity of specific taxa can be measured (Brodie et al., 2007). When using these molecular methods, the extraction protocols, genomic markers, and PCR programs used are crucial factors. Therefore, not standardizing these factors for each sample type and genomic target can lead to a low estimate and only discriminate abundance when sample concentrations differ from 1 to 3 times the order of magnitude (DeLeon-Rodriguez et al. 2013).

On the other hand, in the past decade, genomic sequencing and high-throughput sequencing (HTS) technologies led to a breakthrough in the description of microbial communities in diverse environments (Caporaso et al. 2012). Unlike classical molecular techniques, modern technologies sequence a genomic region hundred or even thousands of times, allowing researchers to detect rare microbial taxa comprising as little as 1% of the original sample (Shokralla et al., 2012). In particular, Illumina platform technology (https://www.illumina.com/) provides paired reads of the same DNA fragment, offers multiplexing capability and generates large amounts of sequence data (Quail et al., 2012). The Illumina MiSeq sequencer has the greatest potential for 16S rDNA sequence studies since it generates long sequence reads (2 $\times$ 300 bp), a significant feature that facilitates assignment to taxonomic groups (Wang et al., 2007). The Illumina MiSeq platform generates 1000-fold more sequences per run than other used HTS technologies, such as the Roche 454 sequencer; deeper sequencing allows better detection and analysis of subdominant and rare bacterial taxa in nature (Caporaso et al. 2012). In addition, it has a performance to cost ratio that is manageable for average-sized research laboratories (Kozich et al., 2013). To our knowledge, the use of other HTS technologies, such as PacBio (https://www.pacb.com/) and Oxford Nanopore (https://nanoporetech.com/), has not been used in the study of bioaerosols in air sample analysis so far. However, it is predicted that more detailed information on airborne bacterial communities will be available in the near future by combining the use of novel multiplex sequencers developed to date.

Using novel techniques for both the isolation of microorganisms and their high-throughput sequencing, a complete characterization of microbial communities is achieved. In addition, the extraction and sequencing of RNA (instead of DNA) allows the study of active bacteria and the exclusion of potentially dead or dormant cells. Interestingly, compared with DNA-based studies, RNA-based studies using 16S rRNA as a target gene have shown differences in the structure and core species in atmospheric bacterial communities (Blazewicz et al., 2013; Klein et al., 2016).

Finally, it is necessary to mention that independent of the method used, the study of airborne bacterial communities also depends on other

factors, such as emission sources (natural and anthropogenic) as well as physicochemical and meteorological conditions, which can play a pivotal role as seasonal influences, determining the variations in the taxonomic compositions and dispersion of airborne bacterial communities in the atmosphere (Monteil et al., 2014; Bertolini et al., 2013). In this context, the most relevant influencing factors identified so far are presented and discussed in the following sections of this review.

3. Abundance and diversity of airborne bacterial communities

As mentioned above, bacteria are one of the most studied bioaerosol components, showing average concentrations from 10^2 to 10^6 cells m^{-3} of air and very high taxonomic diversity (Delort and Amato, 2018; Tanaka et al., 2019). Among airborne prokaryotes, some studies have reported that relative abundance of taxonomic units can be dominated by bacteria (Fröhlich-Nowoisky et al., 2014; Cao et al., 2014). In the same sense, the relative abundance and diversity of bacterial taxonomic units are at least an order of magnitude higher than those of fungi in

Table 1
Taxonomy of the bacteria found in the air according to the environment.

Environment	Phylum	Order	Genus	References
Urban	Proteobacteria	Pseudomonadales	*Pseudomonas*	Bowers et al., 2013; Xu et al., 2017; Liu et al., 2018
		Burkholderiales		
		Rhodospirillales	*Acetobacter*	
		Enterobacteriales	*Salmonella*	
		Legionellales	*Legionella*	
	Bacteroidetes	Sphingobacteriales		
	Firmicutes	Bacillales	*Bacillus*	
		Lactobacillales	*Lactococcus*, *Streptococcus*	
	Actinobacteria	Micrococcales		
		Corynebacteriales	*Corynebacterium*	
	Fusobacteria	Fusobacteriales	*Fusobacterium*	
Suburban	Proteobacteria	Pseudomonadales	*Pseudomonas*	Tanaka et al., 2019; Zhong et al., 2019; Li et al., 2019
		Burkholderiales	*Massilia*, *Ralstonia*	
		Rhizobiales	*Methylobacterium*, *Aureimonas*	
		Sphingomonadales	*Sphingomonas*	
		Enterobacterales	*Pantoea*	
		Rickettsiales	*Rickettsia*	
	Bacteroidetes	Sphingobacteriales		
	Firmicutes	Bacillales	*Bacillus*	
		Lactobacillales	*Lactococcus*, *Carnobacterium*, *Lactobacillus*	
		Clostridiales	*Clostridium*	
	Actinobacteria	Micrococcales	*Micrococcus*	
Rural	Proteobacteria	Pseudomonadales	*Pseudomonas*, *Acinetobacter*	Bowers et al., 2013; Wei et al., 2019a
		Burkholderiales	*Massilia*, *Delftia*, *Janthinobacterium*	
		Rhodospirillales		
		Rhizobiales	*Methylobacterium*	
		Sphingomonadales	*Sphingomonas*	
		Enterobacterales	*Pantoea*	
		Rhodobacterales		
		Caulobacterales	*Brevundimonas*	
		Xanthomonadales	*Stenotrophomonas*	
	Bacteroidetes	Sphingobacteriales	*Pedobacter*	
		Bacteroidales		
	Firmicutes	Bacillales	*Bacillus*	
		Lactobacillales		
		Clostridiales	*Ruminococcus*	
	Actinobacteria	Micrococcales		
		Corynebacteriales	*Corynebacterium*, *Rhodococcus*	
	Acidobacteria			
Mountain	Proteobacteria	Pseudomonadales	*Pseudomonas*, *Acinetobacter*	Tanaka et al., 2019; Wei et al., 2019b
		Burkholderiales	*Massilia*, *Herbaspirillum*, *Polaromonas*, *Ramlibacter*, *Noviherbaspirillum*, *Delftia*, *Janthinobacterium*	
		Rhodospirillales	*Acidiphilium*	
		Rhizobiales	*Bradyrhizobium*, *Methylobacterium*,	
		Sphingomonadales	*Sphingomonas*	
		Xanthomonadales	*Stenotrophomonas*	
	Bacteroidetes	Sphingobacteriales	*Mucilaginibacter*, *Pedobacter*	
		Cytophagales	*Hymenobacter*	
	Firmicutes	Bacillales	*Bacillus*	
	Actinobacteria	Micrococcales	*Micrococcus*	
		Corynebacteriales	*Rhodococcus*	
Coastal	Proteobacteria	Pseudomonadales	*Pseudomonas*, *Acinetobacter*	Michaud et al., 2018; Graham et al., 2018
		Rhizobiales	*Methylobacterium*, *Rhodoplanes*	
		Alteromonadales	*Psychromonas*	
		Vibrionales	*Vibrio*	
	Bacteroidetes	Flavobacteriales	*Flavobacterium*	
	Firmicutes	Bacillales	*Bacillus*, *Staphylococcus*	
		Lactobacillales	*Streptococcus*	
	Actinobacteria	Corynebacteriales	*Rhodococcus*, *Mycobacterium*, *Corynebacterium*	
		Propionibacteriales	*Cutibacterium*	
	Cyanobacteria	Synechococcales	*Synechococcus*	

several environments (Cáliz et al., 2018; Wei et al., 2019a; Tanaka et al., 2019). Moreover, marine mesocosm studies have shown the preferential aerosolization of bacterial cells compared with viral particles (Michaud et al., 2018).

Airborne bacteria may be suspended as individual cells but are more likely to be attached to other particles (soil or leaf fragments) or to be part of microbial biofilms, protecting them against environmental stressors and facilitating their contact and molecular communication (*e.g.*, quorum-sensing) (Delort and Amato, 2018). Approximately 80% higher diversity and relative abundance of bacteria is found on coarse particles (from 2.5 to 10 μm diameter) than on fine particles (<2.5 μm) in both rural and urban areas (Haas et al., 2013; Bowers et al., 2013). However, high bacterial counts, ranging from 10^4 to 10^7 cells m^{-3} of air, have been found in fine and ultrafine fractions of bioaerosols from urban areas, forests, and coastal-industrial and marine areas (Wei et al., 2019b; Whon et al., 2012; Michaud et al., 2018). As a result of their small size (~1 μm), bacterial cells have a relatively long atmospheric residence time (from a few days to several weeks) compared to that of larger particles (Smith et al., 2018). In addition, various bacterial species or strains have high tolerance to low temperature, ultraviolet irradiation, and other environmental stressors that can be encountered in the atmosphere (Klein et al., 2016; DeLeon-Rodriguez et al., 2013; Amato et al., 2015). These bacterial features enable the presence of bacteria in the stratosphere and intercontinental transport over thousands of kilometers (Smith et al., 2018; Maki et al., 2017).

In general terms, the taxonomic affiliation of airborne bacteria (Table 1) has revealed the Proteobacteria group as the most abundant phylum in the air. Within this phylum, the orders Pseudomonadales (*Pseudomonas* and *Acinetobacter*), Burkholderiales (*Massilia*, *Delftia* and *Janthinobacterium*), Rhizobiales (*Methylobacterium)*, Rhodospirillales (*Acetobacter*) and Sphingomonadales (*Sphingomonas*) have been identified as the most representative (Bowers et al., 2013; Zhong et al., 2019; Gandolfi et al., 2013). The Firmicutes orders Bacillales and Lactobacillales, Actinobacteria orders Corynebacteriales and Micrococcales, and Bacteroidetes order Sphingobacteriales are also frequently found in air samples. However, the diversity of airborne bacteria can vary according to sampling area (Table 1). In coastal areas, for example, the Bacteroidetes order Flavobacteriales was more common, whereas in inland areas, the orders Sphingobacteriales, Bacteroidales and Cytophagales were more common (Bowers et al., 2013; Xu et al., 2017; Federici et al., 2018).

As shown in Table 1, specific taxa can be found predominantly in certain rural-agricultural areas relative to other areas, such as urbanized, mountainous and coastal areas. For example, the dominant particle type emitted to the air in rural-agricultural areas is associated with the order Clostridiales and derived from cattle feedlot manure (Bowers et al., 2013; Huang et al., 2013). Higher relative abundance, diversity and richness of airborne bacteria are found in rural areas, followed by urban, suburban, and high-altitude areas (Bowers et al., 2013; Tanaka et al., 2019; Li et al., 2019). This geographical distribution is characterized by the relative contributions of the different bioaerosol emission sources between regions with different urbanization levels (Xie et al., 2018). In rural areas, abundant vegetation and soil can be found; in contrast, urban and suburban areas have a limited and more homogeneous composition of vegetative species. Liu et al. (2019) found that physicochemical factors (PM_{10}, $PM_{2.5}$ and CO) associated with pollution, typically higher in urban than rural areas, increase the similarity of bacterial communities. Higher concentrations of gas pollutants can also provide considerable amounts of nutrients, enabling a high relative abundance of pollutant-degrading bacteria (Wei et al., 2019a). On the other hand, studies have shown that high-altitude mountain areas have two times lower relative abundance and diversity of airborne bacterial communities than suburban and low-altitude areas; however, high-altitude areas can act as a sink for bacteria from low-altitude environments as well as sandstorm clouds and stratospheric and intercontinental transport (Tanaka et al., 2019; DeLeon-Rodriguez et al., 2013; Maki et al., 2019).

Potential and known bacterial pathogens are also present in bioaerosols; most known species are within the genera *Acinetobacter*, *Pseudomonas*, *Staphylococcus*, *Enterococcus*, *Streptococcus*, *Bacillus*, *Bacteroides*, *Burkholderia* and *Vibrio* (Li et al., 2019; Xu et al., 2019). Airborne bacteria linked with severe human health issues, such as *Legionella*, *Salmonella*, and *Bacillus anthracis,* have been identified mostly from dust storms, cities and waste facilities (Liu et al., 2018; Wéry, 2014). In addition, higher diversity and relative abundance of bacterial pathogens can be detected in areas close to wastewater treatment plants and hospital surroundings than areas farther away (Gao et al., 2018; Shimose et al., 2018). In wastewater facilities, the relative abundance (from 0.1% to 23%) and diversity of pathogens increased with successive wastewater treatment steps (Yang et al., 2018). Moreover, sewage sludge application as fertilizers or reclaimed water irrigation can increase bacterial pathogen abundance in urban and suburban areas (Li et al., 2019).

4. Emission sources influencing airborne bacterial communities

As mentioned above, diverse taxa of airborne bacteria can originate from a wide variety of sources (*e.g.*, soils, plant leaves, waterbodies, animal feces, and waste facilities) present in pristine and anthropogenically impacted environments, as schematized in Fig. 2 (Després et al., 2012). The dominant sources of airborne bacteria are terrestrial environments, such as plant leaf surfaces and soils, where bacteria are mostly aerosolized in deserts and dry areas, followed by marine environments, where bacteria on the water surface are aerosolized through sea spray by braking waves or strong winds (Griffin et al., 2017; Smith et al., 2013; Graham et al., 2018). In addition, the type of source (natural or anthropogenic) affects not only the composition of bacterial communities but also the size of the suspended particles in the air and, consequently, the residence time of bioaerosols, since bacteria are mostly attached to suspended particles (Maki et al., 2013).

4.1. Natural sources

Dust plume movements have been widely studied due to positive and negative global impacts. They can cause or aggravate health problems in humans, livestock and agriculture due to their association with and transportation of pathogens and opportunistic microbes, organic compounds and trace metals. The regions of dust mobilization include mostly Saharan and South African, Asian (Gobi Desert), Australian and South American (Atacama Desert) arid regions, which constitute the dust belt (Tomasi et al., 2017). During dust events, the bacterial concentration can increase by one order of magnitude (Maki et al., 2017; Jeon et al., 2011). Bacterial phyla such as Firmicutes (Bacillales), Actinobacteria (Micrococcales and Corynebacteriales) and Bacteroidetes (Sphingobacteriales, Bacteroidales and Flavobacteriales) are the more abundant taxa in desert dust plumes. The Proteobacteria orders more highly correlated with dust plumes are Burkholderiales and the pathogenic Neisseriales (Griffin, 2007). In addition, dust plumes may accumulate bacteria from other environments, such as the well-known aquatic bacterial groups Synechococcales and Vibrionales, (Maki et al., 2017; Abd Aziz et al., 2018).

Volcanic ash is seen as a relevant natural pollutant in the atmosphere. Studies with sterile fresh volcanic ash and high SO_2 exposure have revealed iron-oxidizing bacteria (with high carbon- and nitrogen-fixing activity) as pioneer colonizers (Fujimura et al., 2016; Kerfahi et al., 2017). In mesocosm studies by Kerfahi et al. (2017), where the only apparent source of bacteria was atmospheric deposition or rainfall, bacterial relative abundance was higher in the upper ash layer, whereas greater diversity was found in the lower ash layer. The dominant genera in ashes are members of Acidobacteria (*Blastocatella*), Proteobacteria (*Acinetobacter* and *Burkholderia*) and Bacteroidetes (*Mucilaginibacter* and *Flavisolibacter*). It is widely known that volcanic ash is the basis of a high

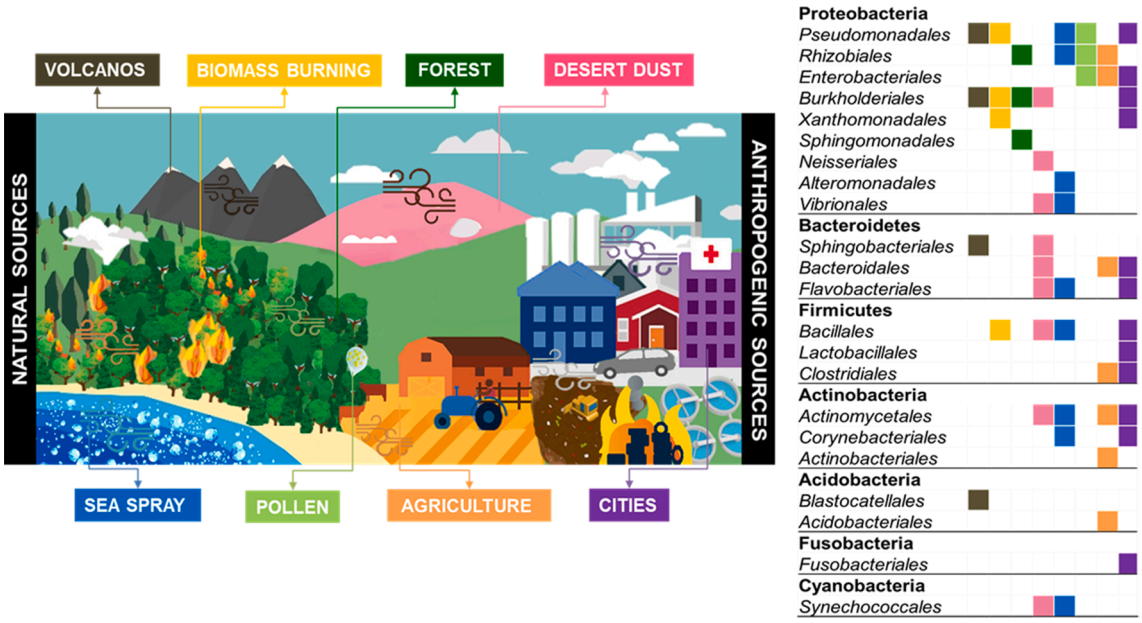

Fig. 2. Schematic of the airborne bacterial orders more associated with different urban and rural sources.

proportion of agricultural soils on earth. Andisols, in which a considerable portion of organic matter is fixed, are derived from the degradation of silicates from volcanic ash. Thus, Gleeson et al. (2006) indicated that bacteria associated with volcanic ash could play a fundamental role in the formation of soils by enhancing chemical degradation and the accumulation of nutrients.

Leaf surfaces and soils have commonly been mentioned as sources of bioaerosols. However, despite the great importance of vegetation to airborne bacterial communities, very few studies have investigated the relationship between the composition of airborne bacteria and vegetation in natural ecosystems (*e.g.*, forests and steppes) and agroecosystems (*e.g.*, pastures, croplands, orchards and plantations). In this context, Bowers et al. (2011, 2013) found that orders such as Burkholderiales, Rhizobiales and Sphingomonadales were dominant in native pine forests as well as urban areas (Denver, USA), leaving uncertainty as to whether the proximity of these forests influences the community found in the city or whether there are other sources for these groups.

Other aspects of vegetation and pollen grains also create microhabitats that allow the establishment of airborne bacteria. Pioneer studies conducted by Manirajan et al. (2018) in different plant species revealed a diverse microbiome associated with pollen, where the most abundant bacterial phyla were Proteobacteria (*e.g.*, Pseudomonadales and Rhizobiales) followed by Firmicutes (*e.g.*, *Bacillus* and *Lactococcus*) and Actinobacteria (*e.g.*, *Curtobacterium* and *Friedmanniella*). Interestingly, different bacterial taxa were correlated with insect (*Rosenbergiella*) and wind pollination (*Methylobacterium*), suggesting that pollination strategy (size, dryness, exine structure and composition) and pollen grain characteristics (hydrophobic coatings and availability of nutrients and life span) can regulate the microbiota associated with different pollen types. Members of the genus *Methylobacterium*, which have a wide variety of features that make them suitable for survival in the atmosphere (desiccation tolerance, nitrogen-fixing activity, biofilm formation, facultative methylotrophy and pigmentation), are often present on pollen and found in air samples (Dourado et al., 2015; Vergara-Fernández et al., 2019). In addition, bacterial species associated with pollen have been found to promote seed germination and as endosymbionts in pine buds. Therefore, it has been postulated that horizontal or vertical bacterial transmission strategies could explain the endophytic and epiphytic seed microbiome (Rodríguez et al., 2018).

Sea sprays also represent one of the largest sources of particles emitted to the atmosphere; their relative mass concentration is formed mainly by chloride (55%), sodium (30%) and sulfate salts (7.7%) and, to a lesser extent, magnesium (3.7%), calcium (1.2%) and potassium (1.1%). Bioaerosols are generated by waves breaking and bubbles bursting in marine waters, enabling the transport of microorganisms from the sea to other nearby terrestrial or aquatic environments (Tomasi et al., 2017). Studies in coastal Pacific seawaters have demonstrated the presence and high aerosolization capacity of several bacterial taxa. The most abundant phyla were Proteobacteria (orders Pseudomonadales, Rhizobiales, Alteromonadales and Vibrionales), Actinobacteria (Micrococcales and Corynebacteriales), Bacteroidetes (Flavobacteriales and Saprospirales), Firmicutes (Bacillales and Lactobacillales) and Cyanobacteria (Synechococcales) (Michaud et al., 2018; Graham et al., 2018).

4.2. Anthropogenic sources

The aerosol emissions from urban activities (*e.g.*, hospitals, houses, pet feces, construction, and transportation), agricultural activities (livestock and farming), and waste treatment facilities (*e.g.*, compost, landfill, and wastewater) constitute important sources of bioaerosols (Delort and Amato, 2018). These are classified as point or diffuse sources when discharges can be traced back to a single source (*e.g.*, waste treatment plants and agricultural activities) or derive from many different sources (*e.g.*, urban activities), respectively (Jones and Harrison, 2004). Although this classification can vary according to the scale utilized, the effects exerted through time in every location and the difficulties in finding specific solutions for one or another source type are highly relevant. Aerosolization from anthropogenic sources is closely associated with movements and aeration processes by the above-mentioned activities. Estimations of bacterial fluxes in the atmosphere are significantly lower in undisturbed than anthropogenically disturbed agroecosystems (Després et al., 2012). For example, wind beyond a threshold velocity is able to aerosolize dominant manure particles in fertilized fields and makes it possible to detect cow fecal bacterial markers in the near-surface atmosphere (Bowers et al., 2013). Studies have also revealed that wastewater treatment plants have high concentrations of airborne bacteria in aeration and agitation systems (Yang et al. 2018; Wéry, 2014).

Although agricultural systems have been mentioned as an important source for airborne bacteria, few studies have focused on their association. Rural-agricultural and associated suburban areas have shown greater dominance of Actinobacteria, Clostridiales and Bacteroidales,

which are associated with livestock feces (Bowers et al., 2011, 2013; Wei et al., 2019a). Likewise, the increase in bioaerosols due to biomass burning (agricultural straw and wildfires) has been mentioned in several studies, but only a few have considered bacterial communities to be associated with these sources. On the North China Plain, Wei et al. (2019a) found that members of the phyla Proteobacteria (orders Pseudomonadales, Xanthomonadales and Burkholderiales) and Firmicutes (Bacillales) significantly increased in samples from burned biomass. Interestingly, in this polluted environment, the total bacterial concentration was one order of magnitude higher and larger interactions (both positive and negative) between microbial taxa (such as bacteria and fungi) and their associations with atmospheric factors (such as carbon, Mg^{2+} and wind speed) were observed.

The occurrence of potentially pathogenic or opportunistic bacteria in the air of wastewater plants has also been detected in several studies (Han et al., 2019; Yang et al., 2018; Degois et al., 2017; Wéry, 2014). The most abundant Proteobacteria were members of the orders Enterobacteriales (genera *Enterobacter*, *Pantoea*, *Escherichia*, *Shigella*, *Klebsiella* and *Serratia*) and Pseudomonadales (*Pseudomonas*, *Acinetobacter* and *Moraxella*). However, other genera important for public and plant health, such as *Alcaligenes*, *Corynebacterium*, *Stenotrophomonas*, *Xanthomonas* and *Legionella*, have also been reported. In China, the relative abundances of pathogens (genera *Bacteroides*, *Burkholderia*, *Enterococcus*, *Staphylococcus*, *Corynebacterium*, *Streptococcus* and *Vibrio*) significantly increased with higher urbanization levels, and samples collected from hospital areas showed the highest pathogen ratios (Li et al., 2019). Companion animals are also a source of bacteria in urban areas, and pathogenic obligate anaerobes such as *Fusobacterium* were found to be characteristic taxa following the aerosolization of dog feces (Bowers et al. 2011).

Finally, it is necessary to mention that the importance of natural and anthropogenic sources of airborne bacterial communities depends not only on geographical location but also on other factors, such as seasonality and changing atmospheric conditions, which can contribute to bacterial dispersion at the local or global level (Bowers et al., 2013). In this sense, atmospheric characteristics, such as meteorological conditions and physicochemical factors, can play a fundamental role in the seasonal variations in airborne bacterial communities; therefore, the next section is focused on these factors.

5. Atmospheric factors influencing airborne bacterial communities

Meteorological conditions and physicochemical factors affect the diversity and dispersion of airborne microbial communities in the atmosphere; however, only a few studies have investigated these relations (Bertolini et al. 2013; Bowers et al. 2013). As Table 2 shows, temperature, relative humidity and wind speed have been identified as the major meteorological factors influencing airborne bacterial communities, whereas the major physicochemical factors have been identified as particle sizes, concentrations and chemical properties. In the following section, in which seasonal differences in the composition of bacterial communities are discussed, the influence of these factors and their changes becomes more apparent (Barberán et al. 2015; Delort and Amato, 2018).

5.1. Meteorological factors

Air temperature is often identified as a factor that significantly shapes the microbial community in different environments and during the four seasons, and studies have shown both inter- and intraseasonal variability (Bertolini et al. 2013; Bowers et al. 2013). Temperature and atmospheric pressure were positively correlated with bacterial diversity by Liu et al. (2018). Notably, air samples collected on days with temperatures below 22 °C in Texas and below 6 °C in Italy were characterized by higher relative abundances of Actinomycetales (Bertolini et al. 2013; Brodie et al. 2007). Lower temperatures have also been associated with an increase in pathogenic bacteria, especially in haze samples (Liu et al., 2018; Cao et al., 2014). It has also been explained that a decrease in temperature stabilizes the atmospheric layer and maintains air pollutants and microbes (Delort and Amato, 2018).

Table 2
Atmospheric factors influencing the composition of airborne bacterial communities.

Meteorological Factors	Physicochemical Factors	References
Temperature*	Nitrogen oxides (NO_x^- and NO_2^-)	Li et al., 2019
Wind speed	Particulate matter (PM_{10})	
Solar radiation	Carbon monoxide (CO)	
	Sulfur dioxide (SO_2)	
Relative humidity	Particulate matter ($PM_{2.5}$)	Zhen et al., 2017
Temperature	Sulfur dioxide (SO_2)	
Wind speed	Ozone (O_3)	
Vapor pressure		
Atmospheric pressure		
Solar radiation		
Relative humidity		Uetake et al., 2019
Wind speed		
Precipitation		
Solar radiation		
Relative humidity	Sulfur dioxide (SO_2)	Gandolfi et al., 2015
Wind speed	Magnesium (Mg^{2+})	
Temperature	Particulate matter (PM_{10} and $PM_{2.5}$)	Li et al., 2018
Relative humidity	Sulfur dioxide (SO_2)	
Atmospheric pressure	Carbon monoxide (CO)	
Wind speed	Ozone (O_3)	
Relative humidity	Sulfur dioxide (SO_2)	Gandolfi et al., 2015
Wind speed	Magnesium (Mg^{2+})	
Temperature		Bowers et al., 2013

* Descendant order of factors in the column denotes the higher relevance according to the cited reference.

Relative humidity and rain have been negatively associated with bacterial diversity since moisture intensifies deposition by increasing particle sizes, and wet soil surfaces make aerosolization unlikely (Gandolfi et al., 2015; Uetake et al., 2019; Smets et al., 2016). Nevertheless, heavy rainfall has been positively associated with an increase in airborne bacterial diversity and humidity, favoring the activity and survival of airborne bacterial concentrations (Zhen et al., 2017; Alghamdi et al., 2014; Dong et al., 2016; Huffman et al., 2013; Uetake et al., 2019). A single raindrop can generate more than 100 bioaerosol droplets smaller than 10 μm, and soil bacteria (*Pseudomonas syringae*, *Bacillus subtilis* and *Corynebacterium glutamicum*) were found to be culturable after 1 h (Joung et al., 2017). The Actinomycetales, Rhizobiales, Sphingomonadales, Pseudomonadales and Enterobacteriales orders were more abundant in samples collected after rainfall, but the Burkholderiales, Lactobacillales and Clostridiales orders were less abundant (Jang et al., 2018). *Salmonella*, an important animal and human pathogen, was found to be maximally aerosolized after 10 min of heavy rain (60 mm h^{-1}) and then deposited in tomato plants (Cevallos-Cevallos et al., 2012). Additionally, heavy rain greatly increased the concentrations of potential ice- and cloud-nucleating bacteria (*e.g., Pseudomonas*) in the air, which can induce rains for up to ~20 days (Monteil et al., 2014; Bigg et al., 2015), causing re-infection of host plants and re-aerosolization of pathogens.

Wind speed has also been positively correlated with the concentration and diversity of bacteria in several studies and associated with an important enhancing factor of bioaerosol generation in soils and on water surfaces, particularly contributing to the formation of sea spray (Wei et al., 2019a; Bowers et al., 2013; Gandolfi et al., 2015). However, strong winds have also been associated with the dilution of local bacterial concentrations, typically in the presence of pollution events (Zhen et al., 2017). The increased use of backwards air trajectory modeling has shown that normal wind patterns can also significantly contribute to the

long-distance dispersion of airborne bacterial communities. In fact, dispersion regimes studied for 20 years suggest that changes in air mass circulation directly affect the expected dispersal of microorganisms and that these effects can occur in a relatively short period (Izquierdo et al., 2012). However, despite several cited studies, the relationship between aerial bacterial community composition and seasonal variation mediated by atmospheric processes is still not well understood or studied in the majority of environments worldwide.

5.2. Physicochemical factors

Airborne bacterial communities are currently studied according to particle size, with higher diversity and concentrations (>50%) found for particles near 2.5 and 10 μm (Gao et al., 2015). Table 3 shows that Proteobacteria are dominant in both fractions, while the orders Rhodospirillales and Enterobacterales are associated with fine particles, and Xanthomonadales, Rhodobacterales, Legionellales, Pasteurellales and Vibrionales are associated with larger particles. In contrast, some bacterial groups, such as Pseudomonadales, Burkholderiales, Rhizobiales and Sphingomonadales, do not show preference for a specific particle size. In the Firmicutes, members of the order Clostridiales are only found on larger particles, but Bacillales and Lactobacillales are found on both sizes as well as in the ultrafine fraction (≤1 μm) (Xu et al., 2017). According to Liu et al. (2018), members of the phylum Bacteroidetes are more commonly associated with fine particles; in contrast, Actinobacteria are more commonly associated with larger particles.

High concentrations of particulate matter and chemical pollutants suspended in the air and derived from biomass burning, vehicle exhaust and fuel combustion can induce haze events (especially during winter) (Tomasi et al., 2017). Studies have suggested that the relative abundance of total and pathogenic bacteria correlates positively with the concentration of particles and pollutants in the air (Zhong et al., 2019). Similarly, bacterial concentrations have also been positively correlated with particulate matter concentrations, since these can act as energy sources, carriers and refuges (Wei et al., 2019a; Haas et al., 2013; Dong et al., 2016; Smets et al., 2016; Zhai et al., 2018). However, with higher concentrations of suspended particles, the correlation between bacteria and particle concentrations can also become negative, especially for smaller particle sizes (Liu et al., 2018; Dong et al., 2016). Chemical composition explains approximately 55% of the variance in bacterial species-environment correlations (Innocente et al., 2017), where the most positively correlated aerosol particles were sulfur (SO_4^{2-} and SO_2), nitrogen (NO_2, NO_3^- and NH_4^+) and carbon (CO and CO_2), followed by K^+, Cl^-, Mg^{2+}, Ca^{2+} and Na^+ (Xu et al., 2017; Zhong et al., 2019; Li et al., 2019).

Undoubtedly, the association of airborne bacterial communities (taking into account the bacterial abundance, diversity and variations in time and space) with particle sizes, haze levels and chemical pollutants is relevant in the study of bioaerosol dispersion processes by physicochemical factors.

5.3. Seasonal variation in airborne bacterial communities

The abovementioned studies indicated relatively large changes in airborne community structure associated with sources and atmospheric factors; these changes follow a pattern for each season (spring, summer, autumn and winter) of the year according to the specific location (or region) (Smets et al., 2016). Although spatial and temporal variations occur within seasons as well as between consecutive days (and even hours within a day), some studies have identified close relationships among seasons, specific atmospheric factors and bacterial communities (Gao et al., 2015). As shown in Table 4, seasonality can be relevant in the taxonomic affiliation of airborne bacteria; thus, plant-associated bacteria (*e.g.*, Sphingomonadales) are identified in warm seasons, whereas during dry and crop-harvesting seasons, soil-inhabiting bacteria (*e.g.*, Actinobacteria and Firmicutes) can prevail (Franzetti et al., 2011; Bowers et al., 2013). Therefore, the dominant sources in each season may be influenced by atmospheric factors, and once the microorganisms are in the atmosphere, factors continue selecting for those taxa with adaptations to maintain their activity. As a result, some taxa can be

Table 3
Taxonomy of the bacteria in the air according to aerosol size.

Sizes	Phylum	Order	Genus	References
Coarse (Larger than 2.5 μm)	Proteobacteria	Pseudomonadales	*Pseudomonas*, *Acinetobacter*	Liu et al., 2018; Yan et al., 2018; Bowers et al., 2013; Zhong et al., 2019
		Burkholderiales	*Burkholderia*	
		Rhizobiales	*Methylobacterium*	
		Sphingomonadales	*Sphingomonas*	
		Xanthomonadales	*Stenotrophomonas**	
		Rhodobacterales	*Paracoccus*	
		Legionellales	*Legionella**	
		Pasteurellales	*Haemophilus**	
		Vibrionales	*Vibrio*	
	Bacteroidetes	Bacteroidales		
	Firmicutes	Bacillales	*Bacillus*, *Staphylococcus*, *Anoxybacillus*	
		Lactobacillales	*Enterococcus**, *Streptococcus*	
		Clostridiales	*Clostridium*	
	Actinobacteria	Micrococcales	*Kocuria*	
		Corynebacteriales	*Mycobacterium*, *Nocardia**	
Fine (Smaller than 2.5 μm)	Proteobacteria	Pseudomonadales	*Pseudomonas*, *Acinetobacter*, *Psychrobacter*	Zhong et al., 2019; Liu et al., 2018; Yan et al., 2018; Xu et al., 2017; Maki et al., 2017
		Burkholderiales	*Rhizobacter*, *Burkholderia*, *Ralstonia*	
		Rhizobiales	*Methylobacterium*	
		Sphingomonadales	*Sphingomonas*	
		Rhodospirillales	*Acetobacter*	
		Enterobacterales	*Klebsiella*, *Enterobacter*, *Shigella*	
	Bacteroidetes	Sphingobacteriales	*Pedobacter*	
		Cytophagales		
		Flavobacteriales	*Myroides*	
	Firmicutes	Bacillales	*Bacillus*, *Anoxybacillus*, *Brochothrix*, *Lysinibacillus*, *Solibacillus*, *Staphylococcus*	
		Lactobacillales	*Lactococcus*, *Lactobacillus*, *Carnobacterium*, *Streptococcus*	
	Actinobacteria	Micrococcales	*Cellulomonas*, *Arthrobacter*	
		Corynebacteriales	*Corynebacterium*	

* Denotes bacterial taxonomic groups found in total aerial suspended particles, suggesting their association with particles >10 μm.

Table 4
Taxonomy of the bacteria in the air according to the season and atmospheric factors.

Seasons	Meteorological Factors	Physicochemical Factors	Phylum	Order	References
Spring	Temperature Relative humidity Wind speed Atmospheric pressure Solar radiation	Nitrogen oxides (NOx^-) Ozone (O_3) Carbon monoxide (CO) Particulate matter ($PM_{2.5}$)	Proteobacteria	Pseudomonadales Burkholderiales Rhodospirillales Rhizobiales Sphingomonadales Rhodobacterales	Bowers et al., 2013; Li et al., 2019; Gandolfi et al., 2015; Zhen et al., 2017
			Firmicutes	Bacillales Clostridiales	
			Deinococcus-Thermus	Deinococcales	
Summer	Relative humidity Vapor pressure Solar radiation	Particulate matter ($PM_{2.5}$, PM_{10}) Carbon monoxide (CO) Ozone (O_3)	Proteobacteria	Pseudomonadales Rhodospirillales Rhizobiales Enterobacteriales	Bowers et al., 2013; Li et al., 2019; Franzetti et al., 2011; Gandolfi et al., 2015; Zhen et al., 2017
			Bacteroidetes	Bacteroidales Sphingobacteriales Chitinophagales	
			Firmicutes	Bacillales Clostridiales Lactobacillales	
			Actinobacteria	Micrococcales	
Autumn	Vapor pressure Relative humidity Wind speed	Particulate matter ($PM_{2.5}$)	Proteobacteria	Burkholderiales Rhizobiales	Bowers et al., 2013; Gandolfi et al., 2015; Li et al., 2018; Zhen et al., 2017
			Bacteroidetes	Bacteroidales Sphingobacteriales	
			Firmicutes	Bacillales Clostridiales	
			Actinobacteria	Micrococcales	
Winter	Atmospheric pressure Wind speed Solar radiation	Sulfur dioxide (SO_2)	Proteobacteria	Pseudomonadales Burkholderiales Rhizobiales Rhodospirillales Rhodobacterales Enterobacteriales Nitrosomonadales	Bowers et al., 2013; Franzetti et al., 2011; Gandolfi et al., 2015; Liu et al., 2018; Xu et al., 2017; Li et al., 2018; Zhen et al., 2017
			Bacteroidetes	Bacteroidales Sphingobacteriales Flavobacteriales	
			Firmicutes	Bacillales Lactobacillales Clostridiales	
			Actinobacteria	Micrococcales	

representative of one or several seasons; however, their proportions as well as their spatial and temporal distributions can change.

The influence of the bacterial sources and their seasonal dependence can be observed in each sampling site. For example, the bacterial concentration between spring and winter among Chinese cities with subtropical and temperate climates varied by three and one order of magnitude, respectively (Xie et al., 2019). More considerable differences are observed in semirural and rural areas, where a higher variety of natural sources provides a higher seasonal concentration and diversity of bacteria compared with that in urban areas, where sources are less varied and more stable during the year (Xie et al., 2018). Moreover, the seasonal trend in total suspended particles was lower than that for finer fractions (PM_{10} and $PM_{2.5}$) (Bertolini et al., 2013; Franzetti et al., 2011), which suggests that taking particle size fractions into account is a necessary step for better characterizations of airborne bacteria.

Bacterial diversity increases with atmospheric temperature and pressure and is positively related to summer and spring conditions. Comparative studies between summer and spring found higher diversities in summer, with more significant variations in rural areas followed by urban and suburban areas (Li et al., 2019). Similar trends were also found for pathogenic bacteria, especially in wastewater treatment plants and areas surrounding hospitals, with a high association with urbanization (Gao et al., 2018; Korzeniewska, 2011; Szyłak-Szydłowski et al., 2016). In autumn and winter samples, significant differences in the richness and diversity of airborne bacteria were found independent of haze level and particle sizes (Bertolini et al. 2013; Franzetti et al. 2011; Yan et al., 2018). Gandolfi et al. (2015) found that the orders Burkholderiales and Actinomycetales were more abundant in colder seasons, while in warmer seasons, Rhodobacterales was more abundant. These findings are in agreement with those of other studies performed in winter, in which the genera *Ralstonia* (Burkholderiales) and *Kocuria* (Micrococcales) increased significantly and were identified as key taxa for interactive networks within airborne bacterial communities.

In contrast with Gandolfi *et al.*, the genera *Rubellimicrobium* and *Paracoccus* (Rhodobacterales) were also found to be abundant and categorized as key taxa in airborne bacterial communities from winter samples (Liu et al., 2018; Yan et al., 2018; Zhong et al., 2019). In Beijing city (China), the highest relative abundance of bacterial pathogens (*Staphylococcus*, *Bacillus*, *Clostridium*, *Enterobacter* and *Klebsiella*) and microbial allergens in winter were found at temperatures $\leq$ 10 °C and humidity $\geq$ 50% (Liu et al., 2018; Cao et al., 2014). Moreover, Li W. et al. (2018) observed variations in distributions according to temperature, with the relative abundances of *Shewanella* and *Halomonas* significantly higher above 0 °C and those of *Klebsiella*, *Ralstonia*, *Prevotella* and *Bacteroides* significantly higher below 0 °C. In contrast, in Seoul city (Korea), bacterial relative abundance increased from autumn

to winter, with an inverse correlation with temperature and humidity (Whon et al., 2012).

Autumn and winter are the seasons in which higher concentrations of particulate matter and chemical pollutants (CO, NO_2 and SO_2) are recorded; this is mainly associated with the use of heaters in houses and stationary atmospheric layers due to temperature decreases and high humidity. In general, compared with autumn, the concentration of Proteobacteria tends to decrease in winter, and the concentrations of Actinobacteria and Firmicutes tend to increase on hazy days. (Liu et al., 2018; Cao et al., 2014). However, haze events can also occur in summer, associated with desert plumes, agricultural biomass burning, traffic and industrial activities. In summer, the relative abundance of Actinobacteria (*Rhodococcus*) was higher on nonhazy days, whereas on hazy days, a higher relative abundance of Firmicutes (*Bacillus*, *Staphylococcus*, *Clostridium*, *Enterococcus and Streptococcus*) was found and Bacteroidetes (Bacteroidales, Sphingobacteriales and Chitinophagales) was predominant (Abd Aziz et al., 2018).

In the last decade, temporal and spatial variations in bacterial communities have been investigated by using HTS approaches (Bertolini et al. 2013; Bowers et al. 2013; Franzetti et al. 2011). Despite the efficiency of HTS technologies, sampling methods play a crucial role in the results; for example, Firmicutes represented almost 90% of the relative abundance when gelatin filters were used for sampling (Li et al., 2019), whereas higher bacterial diversity and Proteobacteria abundance, particularly the genera *Bradyrhizobium* and *Pseudomonas*, were observed with the use of quartz filters (Abd Aziz et al., 2018). Coincidently with the results mentioned in Section 2 of this review, these examples reaffirm the relevance of the sampling and characterization methods used in the study of airborne bacterial communities and how they can bias conclusions.

Despite advances in the study of bioaerosols in natural and anthropogenically impacted areas, many questions related to the diversity, activity and interactions of airborne bacterial communities remain unanswered. In particular, major studies on airborne bacteria and the specific characteristics that support their residence in the atmosphere are needed, as these bacteria are attractive bioprospects due to their ability to produce pigments and tolerate desiccation, and their potentialities in biotechnology are vastly unknown.

6. Activity and bioprospecting of airborne bacterial communities

Despite the extreme conditions, airborne bacteria have adapted and coevolved to survive in the atmosphere owing to a wide variety of specific characteristics and specialized mechanisms, some of which are very attractive for biotechnological applications. Culture-based analyses of airborne bacteria have shown an increase in ribosome production (and thus, their protein synthesis potential) and the transformation of atmospheric compounds such as carbon, nitrogen, and oxidative species (Amato et al., 2007; Vaïtilingom et al., 2013). Studies on microbial activity (measured as the rRNA/rDNA ratio) have revealed that the vast majority of airborne bacterial taxa are potentially active and that less abundant genera can be relevant to the core community (Klein et al., 2016).

Bacteria belonging to the genus *Vibrio*, commonly found in aquatic environments, have been isolated from air samples collected during dust events and show a higher proportion of functional genes involved in iron acquisition (Abd Aziz et al., 2018). Similarly, *Synechococcus*, another water- and dust-associated genus, can not only participate in carbon dioxide cycles, thereby inducing microbial blooms (Hu et al., 2017), but also eliminate excess peroxide from photosynthesis to provide a higher stress tolerance to UV radiation and reactive oxygen species (Maki et al., 2017). Spore-forming and pigmented bacteria are also very attractive for the bioprospecting of and search for novel mechanisms involved in the protection of cells against desiccation and UV radiation, respectively. In this context, pigmented bacteria commonly found in air, such as those from the genera *Pseudomonas*, *Bradyrhizobium* and *Hymenobacter*, represent a source of natural pigments for the textile and food industries (Narsing Rao et al., 2017). Similarly, endospore-forming bacteria belonging to the Firmicutes (Bacillales and Lactobacillales) and Actinobacteria (Actinomycetales) phyla are prevalent in air samples from macroscale dispersion, haze events, and desert dust (Bowers et al., 2011; Federici et al., 2018; Yoo et al., 2019). These bacterial taxa have also been proposed as a tool for the degradation of organic compounds and a source for novel antimicrobial compounds (Xu et al., 2017; Tanaka et al., 2019).

As previously mentioned, the occurrence, proliferation and activity of pathogenic bacteria in the air is a widely studied topic in public health and environmental sciences (Meena et al., 2019; Smets et al., 2016). In this context, pathogenic genera belonging to *Halomonas*, *Shewanella* and *Klebsiella* genera are commonly found in air samples, which also have a great tolerance to high concentrations of nitrate and heavy metals, high salinity, and temperatures below 0 °C (Li W. et al., 2018). Meningitis (*Neisseria meningitidis*) is a clear and well-discussed example of how desert dust movements can provoke disease outbreaks, mainly in the dry season (Polymenakou, 2012). Although pathogens can lose viability in the air, their components or subproducts can remain for long periods. For example, endotoxins (membrane lipopolysaccharides of Gram-negative bacteria) are one of the most well-studied biomolecules, and studies have shown that high concentrations can trigger severe allergic and/or inflammatory reactions and even amplify the immune reaction to air contaminants (Degobbi et al., 2011). The possible role of bacterial endotoxins in pollen-triggered allergies has also been discussed, since bacterial colonization and lipopolysaccharide was observed in pollen (Varga et al., 2013).

Similarly, antibiotic-resistant genes have also been studied in the atmosphere and found to have values of approximately 10^5 copies m^{-3} of air, with higher relative abundance and diversity in hazy outdoor conditions and areas surrounding hospitals (Wang et al., 2019). In this context, Li J. et al. (2018) found a linear correlation between the relative abundance of resistant bacterial genes in the air and cities with high pharmaceutical drug consumption around the world. Interestingly, the dominant antibiotic-resistant genes in the atmosphere were beta-lactam and tetracycline, which were presumably harbored by *Bradyrhizobium* and *Sphingomonas*, respectively (Wang et al., 2019). As aerosols can penetrate into the pulmonary system and transmissibility in the highly dynamic atmosphere could be hastened, airborne antibiotic-resistant genes represent a risk for livestock and public health (Wang et al., 2019). In addition, a study also revealed that the concentration of antibiotic-resistant genes increased with humidity associated with smog (Wang et al., 2019).

The discovery of bacteria in clouds with ice-forming activity opened a new window for research on atmospheric bacterial communities in ecology, environmental science and biotechnology fields. Some bacteria, recognized as plant pathogens that cause cell damage in plant tissues by freezing them, are able to remain active and induce precipitation through cloud, fog and ice formation. The production of ice-binding proteins (with both anti-freezing and ice-nucleating activities) by bacteria regulates the formation or inhibition of ice crystals (Cid et al., 2016; Morris et al., 2014). The genera identified as producers of anti-freezing proteins are *Micrococcus*, *Rhodococcus*, *Pseudomonas* (*P. putida* and *P. fluorescens*), *Moraxella*, *Rhizobium*, *Herbaspirillum*, *Bradyrhizobium* and *Flavobacterium*. In contrast, the ice-nucleating bacteria are *Rhodobacter*, *Pseudomonas* (*P. syringae* and *P. fluorescens*), *Xanthomonas*, *Erwinia* and *Pantoea* (Cid et al., 2016). Other aerosol particles, such as dust and pollen, can act as ice nucleators between −8 °C and −15 °C; however, this activity is carried out by many bacteria between 0 °C and −4 °C. The most efficient bacteria described with ice-nucleating activity at relatively high temperatures so far are those in the genera *Pseudomonas*, *Xanthomonas*, *Erwinia*, and *Pantoea* (Joly et al., 2013). Thus, differences in the activity among ice-nucleating and antifreeze proteins produced by bacteria can have significant effects on agriculture and

climate processes (rainfall and hailstorms). Other industrial uses of these beneficial bacterial groups are food preservation, artificial snow generation and rain inducement in drought-affected regions (Cid et al., 2016; Joly et al., 2013).

Conversely, the abovementioned bacteria, *Halomonas*, *Shewanella* and *Klebsiella*, which have excellent tolerance to pollution, can detoxify arsenic, cadmium, and chromium in contaminated environments (Li W. et al., 2018). The *Methylobacterium* genus can be used to reduce environmental contamination due to its ability to degrade toxic compounds, tolerate high heavy-metal concentrations, and increase plant tolerance to these compounds (Dourado et al., 2015). Methane, one of the most important greenhouse gases emitted from natural and anthropogenic activities, is used as an energy source and degraded by the bacterial genus *Methylobacterium* (Vergara-Fernández et al., 2019). *Methylobacterium* also harbors genes related to plant-bacteria interactions that may be important for developing strains able to promote plant growth and protection against phytopathogens, showing its importance in agriculture and phytoremediation. In addition, Rhodospirillales are frequently found in air samples (DeLeon-Rodriguez et al., 2013; Bowers et al., 2013), showing higher activities despite their low relative abundance (Klein et al., 2016). Members within this bacterial group have demonstrated their capacity to use ethanol as an energy source and organic acids (fumarate, gluconate, lactate, malate, pyruvate, and succinate) as carbon sources (Komagata et al., 2014; Hiraishi et al., 2000). Atmospheric ethanol (from natural and anthropogenic sources) is a precursor of ozone and peroxyacetyl nitrate (an eye irritant found in smog), and succinic acid is often observed in the atmosphere during biomass burning (Vaïtilingom et al., 2011). Coincidently, these studies highlight that airborne bacteria may be involved in the atmospheric biogeochemical cycling of organic compounds relevant to environmental and public health and that their metabolic activity could be applied as biotechnological tools for the bioremediation of contaminated or polluted environments (Al-Bader et al., 2012).

7. Concluding remarks and future perspectives

Although several culture-dependent and culture-independent methods are already being used to unravel the composition and activity of airborne bacterial communities, studies on their sources, atmospheric influencing factors and biotechnological applications are still in their early stages. The heterogeneity of anthropogenic and natural sources as well as the lack of standardized sampling methods may provide inconsistent results and lead to a frustrating lack of robust conclusions about the composition and functions of airborne bacteria in the atmosphere. As shown in the previous sections, there is wide diversity and homogeneity among the most abundant bacterial groups in the atmosphere. However, composition, activity and interactions vary temporally and seasonally according to diverse sources and factors present in each sampling area (Klein et al. 2016; Wei et al. 2019b). These results suggest that a fraction of airborne bacteria may be ubiquitously distributed, perhaps due to long-range dispersion. In contrast, studies could also identify bacterial taxa that may serve as microbial indicators of specific bioaerosol sources and seasonality at the local level. Other authors have also hypothesized the existence of keystone bacterial taxa, which have an impact on ecosystems and local biodiversity, in the atmosphere; this pattern occurs in other extreme and oligotrophic environments, where particular features promote bacterial survival or contribute to the resilience of the ecosystem (DeLeon-Rodriguez et al., 2013). In addition, HTS technologies and omics studies of air microbiology could provide relevant and detailed information on metabolic capacity, activity and connectivity at the DNA, RNA and protein levels. Additionally, adaptations or gene selection as a result of specific atmospheric selective pressure can demonstrate or reveal new gene clusters with great potential for application in biotechnology.

Interestingly, as suggested by Fig. 3, compliance with the WHO standards coincides with the countries with the highest number of studies on bioaerosols. Typically, middle and low-income regions such as Africa, parts of Asia and Latin America are the least well-studied and with lower air quality. In Asian countries such as China and Korea even

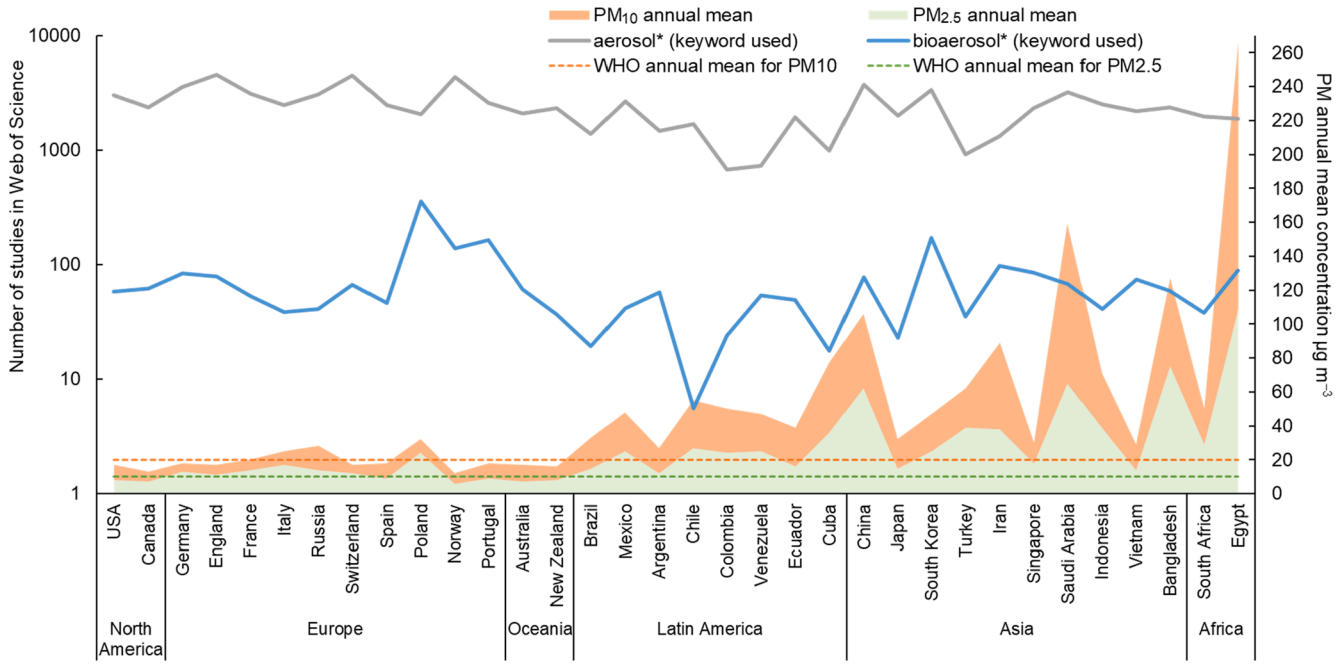

Fig. 3. A search of the number of published studies (until 2019) by country on the Web of Science database using "aerosol" and "bioaerosol" as keywords. The results were normalized against the total number of studies per country using a factor of 10^6. Data from the Global Ambient Air Quality Database (World Health Organization (WHO)) on the PM_{10} and $PM_{2.5}$ annual mean concentrations per country were plotted. The information used is freely downloadable from https://www.who.int/airpollution/data/cities/en/. The dotted lines denote the upper limit of particulate matter proposed by WHO for the PM_{10} and $PM_{2.5}$ annual mean concentrations (World Health Organization, 2006). The search was updated on July 16th, 2020.

with a high number of studies particulate matter levels are above the norm. In these cases, excessive overpopulation, and the high influence of dust from Asian and African deserts, must be taken into account. European countries have high or middle-incomes, a large number of bioaerosol studies and good air quality in general terms; however, some Eastern and Central- Europe countries still do not overcome their pollution problems. As example, Poland has the highest proportion of bioaerosol studies in the Fig. 3, but at the same time, higher particulate matter concentrations are informed due to their huge association to coal mining industry (Environmental European Agency, 2019). In Latin America, it is worth mentioning the case of Chile, which has a high number of aerosol studies, but only one in bioaerosols. Although the Latin American countries of Chile and Argentina have a similar number of studies on aerosols and are both high-income countries, they have contrasting particulate matter concentrations and bioaerosol studies. These results suggest that studies based on the biological fraction of aerosols can have a positive influence on the regulations and policies to mitigate their anthropogenic sources (Grennfelt et al., 2019).

Finally, it is necessary to mention that although bioaerosols and the associated bacteria represent only a part of aerosols, throughout this review, their great abundance, diversity, dynamics and activity in the air from diverse outdoor environments have been exposed. The considerable relevance of bacteria to medical, agricultural, industrial or ecological areas is known, and they are commonly the center of attention for media and social concerns. Undoubtedly, a more in-depth knowledge of the atmospheric microbiome of a particular region or country can contribute to its development on many scales by leading to the proposal of new investigations focused on microbial ecology and the design of efficient regulations and policies for environmental protection and public health.

CRediT authorship contribution statement

Tay Ruiz-Gil: Conceptualization, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Jacquelinne J. Acuña:** Conceptualization, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **So Fujiyoshi:** Writing - review & editing. **Daisuke Tanaka:** Writing - review & editing. **Jun Noda:** Writing - review & editing. **Fumito Maruyama:** Writing - review & editing. **Milko A. Jorquera:** Conceptualization, Investigation, Formal analysis, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

The authors acknowledge to the Editor and two anonymous referees for helpful and constructive criticism of the manuscript.

Funding

The authors thank the financial support given by The National Fund for Scientific and Technological Development (FONDECYT) project no. 1201386 (to J.J.A. and M.A.J.), by Chilean Antarctic Institute (INACH) project code RT_02_16 (to J.J.A. and M.A.J.), by Science and Technology Research Partnership for Sustainable Development (SATREPS JICA/JST) project code JPMJSA1705 (to J.J.A, S.F., F.M. and M.A.J.), by JSPS joint international research KAKENHI-19KK0263 (to D.T., J.N. and F. M.) and Japan Agency for Medical Research and Development AMED 20fk0108129h0501 (to F.M.), by UFRO Scholarship from Universidad de La Frontera (to T.R.G.), and by Program "Apoyo a Profesores Patrocinantes de Alumnos de Pre y Postgrado, Vicerrectoría de Investigación y Postgrado, Universidad de La FronteraVicerrectoría de Investigación y Postgrado, Universidad de La Frontera, code DI19-2016" (to T.R.G.).

References

Abd Aziz, A., Lee, K., Park, B., Park, H., Park, K., Choi, I.G., Chang, I.S., 2018. Comparative study of the airborne microbial communities and their functional composition in fine particulate matter (PM2.5) under non-extreme and extreme PM2.5 conditions. Atmos. Environ. 194, 82–92.

Al-Bader, D., Eliyas, M., Rayan, R., Radwan, S., 2012. Air-dust-borne associations of phototrophic and hydrocarbon-utilizing microorganisms: promising consortia in volatile hydrocarbon bioremediation. Environ Sci Pollut Res 19, 3997–4005.

Alghamdi, M.A., Shamy, M., Redal, M.A., Khoder, M., Awad, A.H., Elserougy, S., 2014. Microorganisms associated particulate matter: A preliminary study. Sci. Total Environ. 479–480, 109–116.

Amato, P., Demeer, F., Melaouhi, A., Fontanella, S., Martin-Biesse, A.-S., Sancelme, M., Laj, P., Delort, A.-M., 2007. A fate for organic acids, formaldehyde and methanol in cloud water: Their biotransformation by microorganisms. Atmos. Chem. Phys. 7, 4159–4169.

Amato, P., Joly, M., Schaupp, C., Attard, E., Möhler, O., Morris, C.E., Brunet, Y., Delort, A.M., 2015. Survival and ice nucleation activity of bacteria as aerosols in a cloud simulation chamber. Atmos. Chem. Phys. 1511, 6455–6465.

Barberán, A., Ladau, J., Leff, J.W., Pollard, K.S., Menninger, H.L., Dunn, R.R., Fierer, N., 2015. Continental-scale distributions of dust-associated bacteria and fungi. Proc. Natl. Acad. Sci. 11218, 5756–5761.

Bertolini, V., Gandolfi, I., Ambrosini, R., Bestetti, G., Innocente, E., Rampazzo, G., Franzetti, A., 2013. Temporal variability and effect of environmental variables on airborne bacterial communities in an urban area of Northern Italy. Appl. Microbiol. Biotechnol. 9714, 6561–6570.

Bigg, E.K., Soubeyrand, S., Morris, C.E., 2015. Persistent after-effects of heavy rain on concentrations of ice nuclei and rainfall suggest a biological cause. Atmos. Chem. Phys. 155, 2313–2326.

Blazewicz, S.J., Barnard, R.L., Daly, R.A., Firestone, M.K., 2013. Evaluating rRNA as an indicator of microbial activity in environmental communities: limitations and uses. ISME J. 7, 2061–2068.

Bowers, R.M., Clements, N., Emerson, J.B., Wiedinmyer, C., Hannigan, M.P., Fierer, N., 2013. Seasonal variability in bacterial and fungal diversity of the near-surface atmosphere. Environ. Sci. Technol. 4721, 12097–12106.

Bowers, R.M., McLetchie, S., Knight, R., Fierer, N., 2011. Spatial variability in airborne bacterial communities across land-use types and their relationship to the bacterial communities of potential source environments. ISME J. 54, 601–612.

Brodie, E.L., DeSantis, T.Z., Parker, J.P.M., Zubietta, I.X., Piceno, Y.M., Andersen, G.L., 2007. Urban aerosols harbor diverse and dynamic bacterial populations. Proc. Natl. Acad. Sci. 1041, 299–304.

Cáliz, J., Triadó-Margarit, X., Camarero, L., Casamayor, E.O., 2018. A long-term survey unveils strong seasonal patterns in the airborne microbiome coupled to general and regional atmospheric circulations. Proc. Natl. Acad. Sci. 11548, 12229–12234.

Camatini, M., Gualtieri, M., Sancini, G., 2017. Impact of the Airborne Particulate Matter on the Human Health. In: Tomasi, C., Fuzzi, S., Kokhanovsky, A.A. (Eds.), Atmospheric Aerosols: Life Cycles and Effects on Air Quality and Climate, pp. 597–643.

Cao, C., Jiang, W., Wang, B., Fang, J., Lang, J., Tian, G., Jiang, J., Zhu, T.F., 2014. Inhalable microorganisms in Beijing's PM2.5 and PM10 pollutants during a severe smog event. Environ. Sci. Technol. 483, 1499–1507.

Caporaso, J.G., Paszkiewicz, K., Field, D., Knight, R., Gilbert, J.A., 2012. The Western English Channel contains a persistent microbial seed bank. ISME J. 6, 1089–1093.

Cevallos-Cevallos, J.M., Gu, G., Danyluk, M.D., Dufault, N.S., Van Bruggen, A.H.C., 2012. Salmonella can reach tomato fruits on plants exposed to aerosols formed by rain. Int. J. Food Microbiol. 1582, 140–146.

Christner, B.C., Cai, R., Morris, C., Mc Carter, K.S., Foreman, C.M., Skidemore, M.L., Montross, S.N., Sands, D.C., 2008. Geographic, seasonal, and precipitation chemistry influence on the abundance and activity of biological ice nucleators in rain and snow. Proc. National Acad. Sci. USA 105, 18854–18859.

Cho, B.C., Hwang, C.Y., 2011. Prokaryotic abundance and 16S rRNA gene sequences detected in marine aerosols on the East Sea Korea. FEMS Microbiol. Ecol. 76, 327–341.

Cid, F.P., Rilling, J.I., Graether, S.P., Bravo, L.A., De La Luz Mora, M., Jorquera, M.A., 2016. Properties and biotechnological applications of ice-binding proteins in bacteria. FEMS Microbiol. Lett. 36311, 1–12.

Degobbi, C., Saldiva, P.H.N., Rogers, C., 2011. Endotoxin as modifier of particulate matter toxicity: a review of the literature. Aerobiologia 272, 97–105.

Degois, J., Clerc, F., Simon, X., Bontemps, C., Leblond, P., Duquenne, P., 2017. First metagenomic survey of the microbial diversity in bioaerosols emitted in waste sorting plants. Ann. Work Exposures Health 619, 1076–1086.

DeLeon-Rodriguez, N., Lathem, T.L., Rodriguez-R, L.M., Barazesh, J.M., Anderson, B.E., Beyersdorf, A.J., Ziemba, L.D., Bergin, M., Nenes, A., Konstantinidis, K.T., 2013. Microbiome of the upper troposphere: species composition and prevalence, effects of tropical storms, and atmospheric implications. Proc. Natl. Acad. Sci. U. S. A. 110 (7), 2575–2580.

Delort, A., Amato, P., 2018. Microbiology of Aerosols. In: Amato, P., Delort, A.-M., (Eds.), John Wiley & Sons, Inc. pp. 320.

Després, V.R., Alex Huffman, J., Burrows, S.M., Hoose, C., Safatov, A.S., Buryak, G., Fröhlich-Nowoisky, J., Elbert, W., Andreae, M.O., Pöschl, U., Jaenicke, R., 2012. Primary biological aerosol particles in the atmosphere: A review. Tellus B 641, 15598.

Dong, L., Qi, J., Shao, C., Zhong, X., Gao, D., Cao, W., Gao, J., Bai, R., Long, G., Chu, C., 2016. Concentration and size distribution of total airborne microbes in hazy and foggy weather. Sci. Total Environ. 541, 1011–1018.
Dourado, M.N., Camargo Neves, A.A., Santos, D.S., Araújo, W.L., 2015. Biotechnological and agronomic potential of endophytic pink-pigmented methylotrophic Methylobacterium spp. BioMed Res Int, 2015.
Duquenne, P., 2018. On the identification of culturable microorganisms for the assessment of biodiversity in bioaerosols. Ann. Work Exposures Health 622, 139–146.
Environmental European Agency (EEA). 2019. Air quality in Europe – 2019 report. Luxembourg: Publications Office of the European Union, 10, 1-104.
Fahlgren, C., Hagström, Å., Nilsson, D., Zweifel, U.L., 2010. Annual variations in the diversity, viability, and origin of airborne bacteria. Appl. Environ. Microbiol. 769, 3015–3025.
Federici, E., Petroselli, C., Montalbani, E., Casagrande, C., Ceci, E., Moroni, B., Porta, G. L., Castellini, S., Selvaggi, R., Sebastiani, B., Crocchianti, S., Gandolfi, I., Franzetti, A., Cappelletti, D., 2018. Airborne bacteria and persistent organic pollutants associated with an intense Saharan dust event in the Central Mediterranean. Sci. Total Environ. 645, 401–410.
Ferguson, R.M.W., Garcia-Alcega, S., Coulon, F., Dumbrell, A.J., Whitby, C., Colbeck, I., 2019. Bioaerosol biomonitoring: Sampling optimization for molecular microbial ecology. Mol. Ecol. Resour. 193, 672–690.
Franzetti, A., Gandolfi, I., Gaspari, E., Ambrosini, R., Bestetti, G., 2011. Seasonal variability of bacteria in fine and coarse urban air particulate matter. Appl. Microbiol. Biotechnol. 902, 745–753.
Fröhlich-Nowoisky, J., Kampf, C.J., Weber, B., Huffman, J.A., Pöhlker, C., Andreae, M. O., Lang-Yona, N., Burrows, S.M., Gunthe, S.S., Elbert, W., Su, H., Hoor, P., Thines, E., Hoffmann, T., Després, V.R., Pöschl, U., 2016. Bioaerosols in the Earth system: Climate, health, and ecosystem interactions. Atmos Res 182, 346–376.
Fröhlich-Nowoisky, J., Ruzene, N.C., Pickersgil, D.A., Galand, P.E., Müller-Germann, I., Nunes, T., Gomes, C.J., Almeida, S.M., Pio, C., Andreae, M.O., Conrad, R., Pöschl, U., Després, V.R., 2014. Diversity and seasonal dynamics of airborne archaea. Biogeosciences 1120, 6067–6079.
Fujimura, R., Kim, S.W., Sato, Y., Oshima, K., Hattori, M., Kamijo, T., Ohta, H., 2016. Unique pioneer microbial communities exposed to volcanic sulfur dioxide. Sci. Rep. 6, 1–9.
Fujiyoshi, S., Tanaka, D., Maruyama, F., 2017. Transmission of airborne bacteria across built environments and its measurement standards: A review. Front. Microbiol. 8 (2336).
Gandolfi, I., Bertolini, V., Ambrosini, R., Bestetti, G., Franzetti, A., 2013. Unravelling the bacterial diversity in the atmosphere. Appl. Microbiol. Biotechnol. 9711, 4727–4736.
Gandolfi, I., Bertolini, V., Bestetti, G., Ambrosini, R., Innocente, E., Rampazzo, G., Papacchini, M., Franzetti, A., 2015. Spatio-temporal variability of airborne bacterial communities and their correlation with particulate matter chemical composition across two urban areas. Appl. Microbiol. Biotechnol. 9911, 4867–4877.
Gao, M., Jia, R., Qiu, T., Han, M., Song, Y., Wang, X., 2015. 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. 118, 203–210.
Gao, X.L., Shao, M.F., Wang, Q., 2018. Airborne microbial communities in the atmospheric environment of urban hospitals in China. J. Hazard. Mater. 349, 10–17.
Gleeson, D.B., Kennedy, N.M., Clipson, N., Melville, K., Gadd, G.M., McDermott, F.P., 2006. Characterization of bacterial community structure on a weathered pegmatitic granite. Microb. Ecol. 51, 526–534.
Graham, K.E., Prussin, A.J., Marr, L.C., Sassoubre, L.M., Boehm, A.B., 2018. Microbial community structure of sea spray aerosols at three California beaches. FEMS Microbiol. Ecol. 943, 1–10.
Grennfelt, P., Engleryd, A., Forsius, M., Hov, Ø., Rodhe, H., Cowling, E., 2019. Acid rain and air pollution : 50 years of progress in environmental science and policy. Ambio.
Griffin, D.W., 2007. Atmospheric movement of microorganisms in clouds of desert dust and implications for human health. Clin. Microbiol. Rev. 203, 459–477.
Griffin, D.W., Gonzalez-Martin, C., Hoose, C., Smith, D.J., 2017. Global-scale atmospheric dispersion of microorganisms. Microbiol. Aerosols 155–194.
Haas, D., Galler, H., Luxner, J., Zarfel, G., Buzina, W., Friedl, H., Marth, E., Habib, J., Reinthaler, F.F., 2013. The concentrations of culturable microorganisms in relation to particulate matter in urban air. Atmos. Environ. 65, 215–222.
Han, Y., Yang, K., Yang, T., Zhang, M., Li, L., 2019. Bioaerosols emission and exposure risk of a wastewater treatment plant with A_2O treatment process. Ecotoxicol. Environ. Saf. 169, 161–168.
Hiraishi, A., Matsuzawa, Y., Kanbe, T., Wakao, N., 2000. Acidisphaera rubrifaciens gen. nov., sp. nov., an aerobic bacteriochlorophyll-containing bacterium isolated from acidic environments. Int. J. Syst. Evol. Microbiol. 50, 1539–1546.
Hu, W., Murata, K., Horikawa, Y., Naganuma, A., Zhang, D., 2017. Bacterial community composition in rainwater associated with synoptic weather in an area downwind of the Asian continent. Sci. Total Environ. 601–602, 1775–1784.
Huang, Q., McConnell, L.L., Razote, E., Schmidt, W.F., Vinyard, B.T., Torrents, A., Hapeman, C.J., Maghirang, R., Trabue, S.L., Prueger, J., Ro, K.S., 2013. Utilizing single particle Raman microscopy as a non-destructive method to identify sources of PM10 from cattle feedlot operations. Atmos. Environ. 66, 17–24.
Huffman, J.A., Prenni, A.J., Demott, P.J., Pöhlker, C., Mason, R.H., Robinson, N.H., Fröhlich-Nowoisky, J., Tobo, Y., Després, V.R., Garcia, E., Gochis, D.J., Harris, E., Müller-Germann, I., Ruzene, C., Schmer, B., Sinha, B., Day, D.A., Andreae, M.O., Jimenez, J.L., Gallagher, M., Kreidenweis, S.M., Bertram, A. K., Pöschl, U., 2013. High concentrations of biological aerosol particles and ice nuclei during and after rain. Atmospheric Chem. Phys. 1313, 6151–6164.
Innocente, E., Squizzato, S., Visin, F., Facca, C., Rampazzo, G., Bertolini, V., Gandolfi, I., Franzetti, A., Ambrosini, R., Bestetti, G., 2017. Influence of seasonality, air mass origin and particulate matter chemical composition on airborne bacterial community structure in the Po Valley. Italy. Sci. Total Environ. 593, 677–687.
Izquierdo, R., Avila, A., Alarcón, M., 2012. Trajectory statistical analysis of atmospheric transport patterns and trends in precipitation chemistry of a rural site in NE Spain in 1984–2009. Atmos Environ. 61, 400–408.
Jang, G.I., Hwang, C.Y., Cho, B.C., 2018. Effects of heavy rainfall on the composition of airborne bacterial communities. Front. Environ. Sci. Eng. 122, 1–10.
Jeon, E.M., Kim, H.J., Jung, K., Kim, J.H., Kim, M.Y., Kim, Y.P., Ka, J.O., 2011. Impact of Asian dust events on airborne bacterial community assessed by molecular analyses. Atmos. Environ. 45, 4313–4321.
Joly, M., Attard, E., Sancelme, M., Deguillaume, L., Guilbaud, C., Morris, C.E., Amato, P., Delort, A.M., 2013. Ice nucleation activity of bacteria isolated from cloud water. Atmos. Environ. 70, 392–400.
Jones, A.M., Harrison, R.M., 2004. The effects of meteorological factors on atmospheric bioaerosol concentrations - A review. Sci. Total Environ. 326, 151–180.
Joung, Y.S., Ge, Z., Buie, C.R., 2017. Bioaerosol generation by raindrops on soil. Nat. Commun. 81, 14668.
Kerfahi, D., Tateno, R., Takahashi, K., Cho, H.J., Kim, H., Adams, J.M., 2017. Development of soil bacterial communities in volcanic ash microcosms in a range of climates. Microb. Ecol. 73, 775–790.
Kim, K.H., Kabir, E., Jahan, S.A., 2018. Airborne bioaerosols and their impact on human health. J. Environ. Sci. 67.
Klein, A.M., Bohannan, B.J.M., Jaffe, D.A., Levin, D.A., Green, J.L., 2016. Molecular evidence for metabolically active bacteria in the atmosphere. Front. Microbiol. 1–11.
Komagata, K., Iino, T., Yamada, Y., 2014. The family Acetobacteraceae. In: Rosenberg, E., DeLong, E., Lory, S., Stackebrandt, E., Thompson, F. (Eds.), The Prokaryotes SE – 396. Springer, Berlin, pp 3–78.
Korzeniewska, E., 2011. Emission of bacteria and fungi in the air from wastewater treatment plants - a review. Front. Biosci. 3, 393–407.
Kozich, J.J., Westcott, S.L., Baxter, N.T., Highlander, S.K., Schloss, P.D., 2013. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. Appl. Environ. Microbiol. 79, 5112–5120.
Li, H., Zhou, X.Y., Yang, X.R., Zhu, Y.G., Hong, Y.W., Su, J.Q., 2019. Spatial and seasonal variation of the airborne microbiome in a rapidly developing city of China. Sci. Total Environ. 665, 61–68.
Li, J., Cao, J.J., Zhu, Y.G., Chen, Q.L., Shen, F.X., Wu, Y., Xu, S.Y., Fan, H., Da, G., Huang, R.J., Wang, J., de Jesus, A.L., Morawska, L., Chan, C.K., Peccia, J., Yao, M.S., 2018a. Global survey of antibiotic resistance genes in air. Environ. Sci. Technol. 52, 10975–10984.
Li, W., Yang, J., Zhang, D., Li, B., Wang, E., Yuan, H., 2018b. Concentration and community of airborne bacteria in response to cyclical haze events during the fall and midwinter in Beijing, China. Front Microbiol 9, 1–12.
Liu, H., Hu, Z., Zhou, M., Hu, J., Yao, X., Zhang, H., Li, Z., Lou, L., Xi, C., Qian, H., Li, C., Xu, X., Zheng, P., Hu, B., 2019. The distribution variance of airborne microorganisms in urban and rural environments. Environ. Pollut. 247, 898–906.
Liu, H., Zhang, X., Zhang, H., Yao, X., Zhou, M., Wang, J., He, Z., Zhang, H., Lou, L., Mao, W., Zheng, P., Hu, B., 2018. Effect of air pollution on the total bacteria and pathogenic bacteria in different sizes of particulate matter. Environ. Pollut. 233, 483–493.
Luhung, I., Wu, Y., Ng, C.K., Miller, D., Cao, B., Chang, V.W.C., 2015. Protocol improvements for low concentration DNA-based bioaerosol sampling and analysis. PLoS One, 1011.
Maki, T., Bin, C., Kai, K., Kawai, Kei, Fujita, K., Ohara, K., Kobayashi, F., Davaanyan, E., Noda, J., Minamoto, Y., Shi, G., Hasegawa, H., Iwasaka, Y., 2019. Vertical distributions of airborne microorganisms over Asian dust source region of Taklimakan and Gobi Desert. Atmos. Environ. 214, 116848.
Maki, T., Hara, K., Iwata, A., Lee, K.C., Kawai, K., Kai, K., Kobayashi, F., Pointing, S.B., Archer, S., Hasegawa, H., Iwasaka, Y., 2017. Variations in airborne bacterial communities at high altitudes over the Noto Peninsula Japan in response to Asian dust events. Atmos. Chem. Phys. 17, 11877–11897.
Maki, T., Kakikawa, M., Kobayashi, F., Yamada, M., Matsuki, A., Hasegawa, H., Iwasaka, Y., 2013. Assessment of composition and origin of airborne bacteria in the free troposphere over Japan. Atmos. Environ. 74, 73–82.
Manirajan, B.A., Maisinger, C., Ratering, S., Rusch, V., Schwiertz, A., Cardinale, M., Schnell, S., 2018. Diversity, specificity, co-occurrence and hub taxa of the bacterial-fungal pollen microbiome. FEMS Microbiol. Ecol. 948.
Martiny, A.C., 2019. High proportions of bacteria are culturable across major biomes. ISME J. 3–6.
Meena, M., Swapnil, P., Barupal, T., Sharma, K., 2019. A review on infectious pathogens and mode of transmission. J. Plant Pathol. Microbiol. 101, 1–4.
Michaud, J.M., Thompson, L.R., Kaul, D., Espinoza, J.L., Richter, R.A., Xu, Z.Z., Lee, C., Pham, K.M., Beall, C.M., Malfatti, F., Azam, F., Knight, R., Burkart, M.D., Dupont, C. L., Prather, K.A., 2018. Taxon-specific aerosolization of bacteria and viruses in an experimental ocean-atmosphere mesocosm. Nat. Commun. 9 (2017).
Monteil, C.L., Bardin, M., Morris, C.E., 2014. Features of air masses associated with the deposition of Pseudomonas syringae and Botrytis cinerea by rain and snowfall. ISME J. 811, 2290–2304.
Morris, C.E., Leyronas, C., Nicot, P.C., 2014. Movement of bioaerosols in the atmosphere and the consequences for climate and microbial evolution. In: Colbeck, I., Lazaridis, M. (Eds.), Aerosol Science, pp. 393–415.
Narsing Rao, M.P., Xiao, M., Li, W.J., 2017. Fungal and bacterial pigments: secondary metabolites with wide applications. Front. Microbiol. 8, 1113.

Peccia, J., Hernandez, M., 2006. Incorporating polymerase chain reaction-based identification, population characterization, and quantification of microorganisms into aerosol science: A review. Atmos. Environ. 4021, 3941–3961.
Polymenakou, P.N., 2012. Atmosphere: A source of pathogenic or beneficial microbes? Atmosphere 31, 87–102.
Quail, M.A., Smith, M., Coupland, P., Otto, T.D., Harris, S.R., Connor, T.R., Bertoni, A., Swerdlow, H.P., Gu, Y., 2012. A tale of three next generation sequencing platforms: comparison of Ion Torrent, Pacific Biosciences and Illumina MiSeq sequencers. BMC Genomics 13, 341.
Ravva, S.V., Hernlem, B.J., Sarreal, C.Z., Mandrell, R.E., 2012. Bacterial communities in urban aerosols collected with wetted-wall cyclonic samplers and seasonal fluctuations of live and culturable airborne bacteria. J Environ Monit 14, 473–481.
Rodríguez, C.E., Mitter, B., Barret, M., Sessitsch, A., Compant, S., 2018. Commentary: seed bacterial inhabitants and their routes of colonization. Plant Soil 4221–4222, 129–134.
Šantl-Temkiv, T., Gosewinkel, U., Starnawski, P., Lever, M., Finster, K., 2018. Aeolian dispersal of bacteria in southwest Greenland: their sources, abundance, diversity and physiological states. FEMS Microbiol. Ecol. 944, 1–10.
Shimose, L.A., Masuda, E., Caban, A.B., Muñoz-Price, L.S., 2018. Air contamination in the hospital environment. In: Bearman, G., Munoz-Price, S., Morgan, D.J., Murthy, R. K. (Eds.), Infection Prevention: New Perspectives and Controversies. Springer International Publishing, Cham, pp. 163–172.
Shokralla, S., Spall, J.L., Gibson, J.F., Hajibabaei, M., 2012. Next-generation sequencing technologies for environmental DNA research. Mol Ecol 21, 1794–1805.
Smets, W., Moretti, S., Denys, S., Lebeer, S., 2016. Airborne bacteria in the atmosphere: Presence, purpose, and potential. Atmos. Environ. 139, 214–221.
Smith, D.J., Ravichandar, J.D., Jain, S., Griffin, D.W., Yu, H., Tan, Q., Thissen, J., Lusby, T., Nicoll, P., Shedler, S., Martinez, P., Osorio, A., Lechniak, J., Choi, S., Sabino, K., Iverson, K., Chan, L., Jaing, C., McGrath, J., 2018. Airborne bacteria in earth's lower stratosphere resemble taxa detected in the troposphere: Results from a new NASA Aircraft Bioaerosol Collector ABC. Front. Microbiol. 9, 1–20.
Smith, D.J., Timonen, H.J., Jaffe, D.A., Griffin, D.W., Birmele, M.N., Perry, K.D., Ward, P. D., Roberts, M.S., 2013. Intercontinental dispersal of bacteria and archaea by transpacific winds. Appl. Environ. Microbiol. 79 (4), 1134–1139.
Szyłak-Szydłowski, M., Kulig, A., Miaśkiewicz-Pęska, E., 2016. Seasonal changes in the concentrations of airborne bacteria emitted from a large wastewater treatment plant. Int. Biodeterioration Biodegradation. 115, 11–16.
Tanaka, D., Fujiyoshi, S., Maruyama, F., Goto, M., Koyama, S., Kanatani, J., Isobe, J., Watahiki, M., Sakatoku, A., Kagaya, S., Nakamura, S., 2020. Size resolved characteristics of urban and suburban bacterial bioaerosols in Japan as assessed by 16S rRNA amplicon sequencing. Sci. Rep. 10 (12406), 1–10.
Tanaka, D., Sato, K., Goto, M., Fujiyoshi, S., Maruyama, F., Takato, S., Shimada, T., Sakatoku, A., Aoki, K., Nakamura, S., 2019. Airborne microbial communities at high-altitude and suburban sites in Toyama, Japan suggest a new perspective for bioprospecting. Front. Bioeng. Biotechnol. 7, 12.
Tang, L., Nagashima, T., Hasegawa, K., Ohara, T., Sudo, K., Itsubo, N., 2018. Development of human health damage factors for PM2.5 based on a global chemical transport model. Int. J. Life Cycle Assess 2312, 2300–2310.
Temkiv, T.S., Finster, K., Hansen, B.M., Nielsen, N.W., Karlson, U.G., 2012. The microbial diversity of a storm cloud as assessed by hailstones. FEMS Microbiol. Ecol. 81, 684–695.
Tomasi, C., Fuzzi, S., Kokhanovsky, A. (Eds.), 2017. Atmospheric Aerosols: Life Cycles and Effects on Air Quality and Climate. John Wiley & Sons, First, pp. 704.
Uetake, J., Tobo, Y., Uji, Y., Hill, T.C.J., DeMott, P.J., Kreidenweis, S.M., Misumi, R., 2019. Seasonal changes of airborne bacterial communities over Tokyo and influence of local meteorology. Front. Microbiol. 10 (1572).
Vaïtilingom, M., Attard, E., Gaiani, N., Sancelme, M., Deguillaume, L., Flossmann, A.I., Amato, P., Delort, A.M., 2012. Long-term features of cloud microbiology at the puy de Dôme France. Atmos Environ 56, 88–100.
Vaïtilingom, M., Charbouillot, T., Deguillaume, L., Maisonobe, R., Parazols, M., Amato, P., Sancelme, M., Delort, A.M., 2011. Atmospheric chemistry of carboxylic acids: microbial implication versus photochemistry. Atmospheric Chem. Phys. 11, 8721–8733.
Vaïtilingom, M., Deguillaume, L., Vinatier, V., Sancelme, M., Amato, P., Chaumerliac, N., Delort, A.M., 2013. Potential impact of microbial activity on the oxidant capacity and organic carbon budget in clouds. Proc. Natl. Acad. Sci. U.S.A. 110, 559–564.
Varga, A., Budai, M.M., Milesz, S., Bácsi, A., Tozsér, J., Benko, S., 2013. Ragweed pollen extract intensifies lipopolysaccharide-induced priming of NLRP3 inflammasome in human macrophages. Immunology 1384, 392–401.
Vergara-Fernández, A., Morales, P., Scott, F., Guerrero, S., Yañez, L., Mau, S., Aroca, G., 2019. Methane biodegradation and enhanced methane solubilization by the filamentous fungi Fusarium solani. Chemosphere 24–35.
Wang, Q., Garrity, G.M., Tiedje, J.M., Cole, J.R., 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Appl. Environ. Microbiol. 73, 5261–5267.
Wang, Y., Wang, C., Song, L., 2019. Distribution of antibiotic resistance genes and bacteria from six atmospheric environments: Exposure risk to human. Sci. Total Environ. 694, 133750.
Wei, M., Xu, C., Xu, X., Zhu, C., Li, J., Lv, G., 2019a. Characteristics of atmospheric bacterial and fungal communities in PM 2.5 following biomass burning disturbance in a rural area of North China Plain. Sci. Total Environ. 651, 2727–2739.
Wei, M., Xu, C., Xu, X., Zhu, C., Li, J., Lv, G., 2019b. Size distribution of bioaerosols from biomass burning emissions: Characteristics of bacterial and fungal communities in submicron PM 1.0 and fine PM 2.5 particles. Ecotoxicol. Environ. Saf. 171, 37–46.
Wéry, N., 2014. Bioaerosols from composting facilities-a review. Front. Cell. Infect. Microbiol. 4, 1–9.
Whon, T.W., Kim, M.-S., Roh, S.W., Shin, N.-R., Lee, H.-W., Bae, J.-W., 2012. Metagenomic characterization of airborne viral DNA diversity in the near-surface atmosphere. J. Virol. 8615, 8221–8231.
World Health Organization. 2006. Air quality guidelines global update 2005: particulate matter, ozone, nitrogen dioxide and sulfur dioxide. Copenhagen: WHO Regional Office for Europe. https://apps.who.int/iris/handle/10665/107823.
Xie, J., Jin, L., He, T., Chen, B., Luo, X., Feng, B., Huang, W., Li, J., Pingqing, F., Li, X., 2019. Bacteria and antibiotic resistance genes ARGs in PM 2.5 from China: implications for human exposure. Environ. Sci. Technol. 532, 963–972.
Xie, J., Jin, L., Luo, X., Zhao, Z., Li, X., 2018. Seasonal disparities in airborne bacteria and associated antibiotic resistance genes in PM2.5 between urban and rural sites. Environ. Sci. Technol. Lett. 52, 74–79.
Xu, C., Wei, M., Chen, J., Wang, X., Zhu, C., Li, J., Zheng, L., Sui, G., Li, W., Wang, W., Zhang, Q., Mellouki, A., 2017. Bacterial characterization in ambient submicron particles during severe haze episodes at Ji'nan, China. Sci. Total Environ. 580, 188–196.
Xu, C., Wei, M., Chen, J., Zhu, C., Li, J., Xu, X., Wang, W., Zhang, Q., Ding, A., Kane, H., Zhao, Z., Mellouki, A., 2019. Profile of inhalable bacteria in PM 2.5 at Mt. Tai, China: Abundance, community, and influence of air mass trajectories. Ecotoxicol. Environ. Saf. 168, 110–119.
Yan, D., Zhang, T., Su, J., Zhao, L.-L., Wang, H., Fang, X.-M., Zhang, Y.-Q., Liu, H.-Y., Yua, L.-Y., 2018. Structural variation in the bacterial community associated with airborne particulate matter in Beijing, China, during Hazy and Nonhazy Days. Appl. Environ. Microbiol. 849, 1–13.
Yang, K., Li, L., Wang, Y., Xue, S., Han, Y., Liu, J., 2018. Airborne bacteria in a wastewater treatment plant: Emission characterization, source analysis and health risk assessment. Water Res. 596–606.
Yoo, K., Han, I., Ko, K.S., Lee, T.K., Yoo, H., Khan, M.I., Tiedje, J.M., Park, J., 2019. Bacillus-dominant airborne bacterial communities identified during Asian dust events. Microb. Ecol. 78677, 1–11.
Zhai, Y., Li, X., Wang, T., Wang, B., Li, C., Zeng, G., 2018. A review on airborne microorganisms in particulate matters: Composition, characteristics and influence factors. Environ. Int. 113, 74–90.
Zhen, Q., Deng, Y., Wang, Y., Wang, X., Zhang, H., Sun, X., Ouyang, Z., 2017. Meteorological factors had more impact on airborne bacterial communities than air pollutants. Sci. Total Environ. 601–602, 703–712.
Zhong, S., Zhang, L., Jiang, X., Gao, P., 2019. Comparison of chemical composition and airborne bacterial community structure in PM 2.5 during haze and non-haze days in the winter in Guilin, China. Sci. Total Environ. 655, 202–210.