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Invited review article

Bioaerosols in the Earth system: Climate, health, and ecosystem interactions

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ABSTRACT

Aerosols of biological origin play a vital role in the Earth system, particularly in the interactions between atmosphere, biosphere, climate, and public health. Airborne bacteria, fungal spores, pollen, and other bioparticles are essential for the reproduction and spread of organisms across various ecosystems, and they can cause or enhance human, animal, and plant diseases. Moreover, they can serve as nuclei for cloud droplets, ice crystals, and precipitation, thus influencing the hydrological cycle and climate. The sources, abundance, composition, and effects of biological aerosols and the atmospheric microbiome are, however, not yet well characterized and constitute a large gap in the scientific understanding of the interaction and co-evolution of life and climate in the Earth system. This review presents an overview of the state of bioaerosol research, highlights recent advances, and outlines future perspectives in terms of bioaerosol identification, characterization, transport, and transformation processes, as well as their interactions with climate, health, and ecosystems, focusing on the role bioaerosols play in the Earth system.

Contents

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1. Introduction

Primary biological aerosols (PBA), in short bioaerosols, are a subset of atmospheric particles, which are directly released from the biosphere into the atmosphere. They comprise living and dead organisms (e.g., algae, archaea, bacteria), dispersal units (e.g., fungal spores and plant pollen), and various fragments or excretions (e.g., plant debris and brochosomes; Ariya and Amyot, 2004; Brown et al., 1964; Castillo et al., 2012; Cox and Wathes, 1995; Després et al., 2012; Graham, 2003; Madelin, 1994; Matthias-Maser et al., 1995; Rogerson and Detwiler, 1999; Tesson et al., 2016; Womack et al., 2010). As illustrated in Fig. 1, PBA particle diameters range from nanometers up to about a tenth of a millimeter. The upper limit of the aerosol particle size range is determined by rapid sedimentation, i.e., larger particles are too heavy to remain airborne for extended periods of time (Hinds, 1999; Pöschl, 2005).

Historically, the first investigations of the occurrence and dispersion of microorganisms and spores in the air can be traced back to the early 19th century (Ehrenberg, 1830; Pasteur, 1860a, 1860b). Since then, the study of bioaerosol has come a long way, and air samples collected with aircraft, balloons, and rockets have shown that PBA released from land and ocean surfaces can be transported over long distances and up to very high altitudes, i.e., between continents and beyond the troposphere (Brown and Hovmøller, 2002; DeLeon-Rodriguez et al., 2013; Elbert et al., 2007; Gregory, 1945; Griffin et al., 2001; Griffin, 2004; Hallar et al., 2011; Hirst et al., 1967; Imshenetsky et al., 1978; Maki et al., 2013; McCarthy, 2001; Pady et al., 1950; Polymenakou et al., 2007; Pósfai et al., 2003; Proctor, 1934; Prospero et al., 2005; Scheppegrell, 1924; Shivaji et al., 2006; Smith et al., 2013; Wainwright et al., 2003).

Bioaerosols play a key role in the dispersal of reproductive units from plants and microbes (pollen, spores, etc.), for which the atmosphere enables transport over geographic barriers and long distances (e.g., Brown and Hovmøller, 2002; Burrows et al., 2009a, 2009b; Després et al., 2012; Womack et al., 2010). Bioaerosols are thus highly relevant for the spread of organisms, allowing genetic exchange between habitats and geographic shifts of biomes. They are central elements in the development, evolution, and dynamics of ecosystems.

The dispersal of plant, animal, and human pathogens and allergens has major implications for agriculture and public health (e.g., Adhikari et al., 2006; Brodie et al., 2007; Brown and Hovmøller, 2002; Després et al., 2012; Douwes, 2003; Fisher et al., 2012; Fröhlich-Nowoisky et al., 2009; Gorny et al., 2002; Kellogg and Griffin, 2006), and the potential impacts of airborne transmission of genetically modified organisms are under discussion (e.g., Angevin et al., 2008; Folloni et al., 2012; Kawashima and Hama, 2011). Moreover, bioaerosols can serve as nuclei for cloud droplets, ice crystals, and precipitation, thus influencing the hydrological cycle and climate. Especially in pristine air over vegetated regions, bioaerosols are likely to be an essential regulating factor in the formation of precipitation and vice versa (e.g., DeLeon-Rodriguez et al., 2013; Huffman et al., 2013; Möhler et al., 2007; Morris et al., 2014a; Pöschl et al., 2010; Prenni et al., 2013; Sands et al., 1982; Schnell and Vali, 1972; Sesartic et al., 2013; Tobo et al., 2013; Vali et al., 1976). Also in marine environments, particulate matter of biological origin may contribute substantially to the abundance of ice nuclei (Alpert et al., 2011a; Burrows et al., 2013a; Knopf et al., 2010; Lee et al., 2015; Parker et al., 1985; Schnell and Vali, 1976; Schnell and Vali, 1975; Schnell, 1975; Wilson et al., 2015).

An overview of bioaerosol cycling and effects in the Earth system is given in Fig. 2. Some organisms actively emit PBA particles, such as wet-discharged fungal spores, which are emitted with the help of osmotic pressure or surface tension effects, while the passive emission of other PBA particles, like thallus fragments and dry-discharged fungal spores, is mostly wind-driven (Elbert et al., 2007). In the atmosphere, PBA undergo internal and external mixing with other aerosols, including biogenic secondary organic aerosol (SOA) formed upon oxidation and gas-to-particle conversion of biogenic volatile organic compounds, which can influence bioaerosol properties through SOA coatings on PBA particles (Hallquist et al., 2009; Huffman et al., 2012; Pöhlker et al., 2012b; Pöschl et al., 2010).

In the course of atmospheric transport, bioaerosols undergo further chemical and physical transformation, stress, and biological aging upon interaction with UV radiation, photo-oxidants, and various air pollutants like acids, nitrogen oxides, aromatic compounds, and soot (Estillore et al., 2016; Franze et al., 2005; Santarpia et al., 2012; Shiraiwa et al., 2012b). Particle transformation and aging also occur

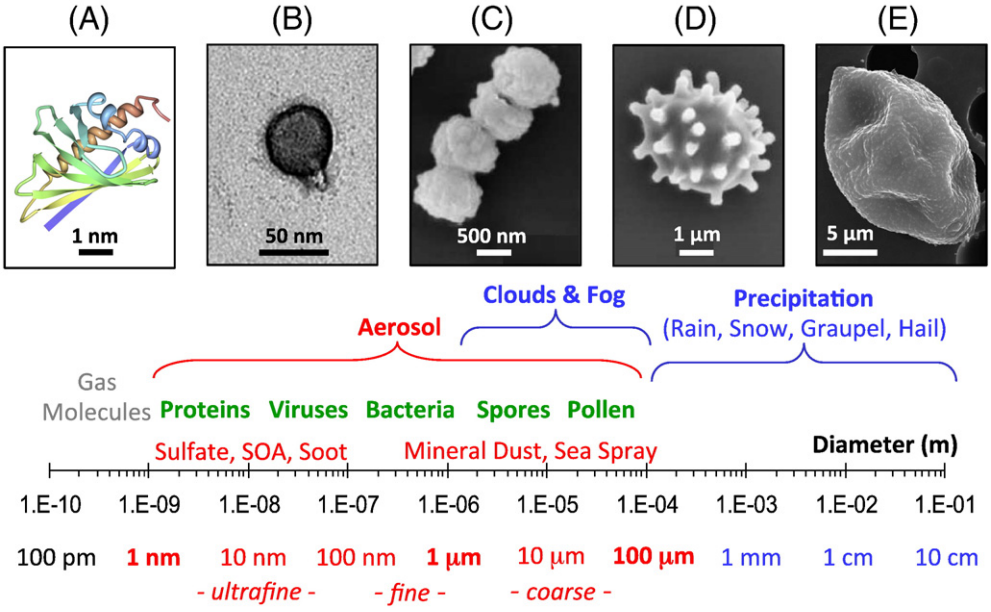

Fig. 1. Characteristic size ranges of atmospheric particles and bioaerosols with exemplary illustrations: (A) protein, (B) virus, (C) bacteria, (D) fungal spore, and (E) pollen grain (adapted from Pöschl and Shiraiwa, 2015). Image A is a model simulation of BetV1 (Kofler et al., 2012; Xu and Zhang, 2009) created with PDB protein workshop 3.9 (Moreland et al., 2005). Images (B–E) are scanning electron micrographs of representative particles from each of the bioaerosol categories listed. Image B reprinted from Whon et al. (2012), copyright 2012, with permission from American Society for Microbiology. Images C and D reprinted from Wittmaack et al. (2005), copyright 2005, with permission from Elsevier. Image E reprinted from Valsan et al. (2015), copyright 2015, with permission from Elsevier.

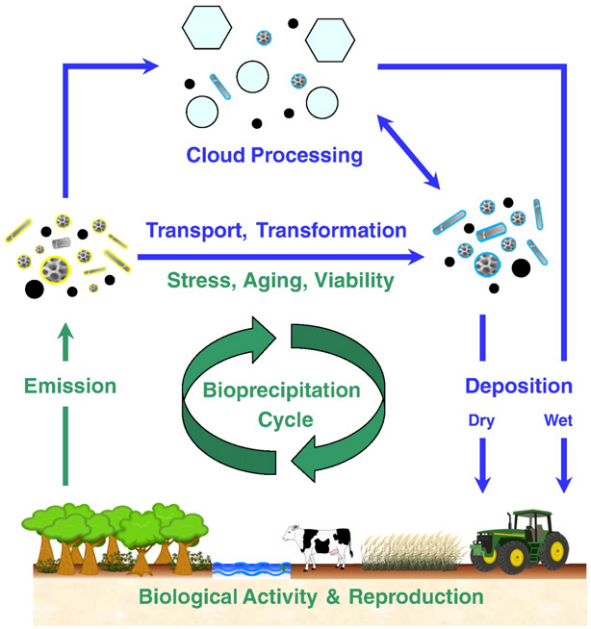

Fig. 2. Bioaerosol cycling in the Earth system. After emission from the biosphere, bioaerosol particles interact with other aerosol particles and trace gases in the atmosphere and can be involved in the formation of clouds and precipitation. After dry or wet deposition to the Earth's surface, viable bioparticles can contribute to biological reproduction and further emission. This feedback can be particularly efficient when coupled to the water cycle (bioprecipitation).
Adapted from Pöschl and Shiraiwa (2015) and Pöschl (2005).

upon cloud processing, i.e., when cloud droplets or ice crystals form on or scavenge bioaerosol particles. Most clouds re-evaporate and release modified particles, but when they form precipitation that reaches the Earth's surface, not only condensation and ice nuclei but also other aerosol particles are scavenged on the way to the surface and removed from the atmosphere. This process of "wet deposition" is the major sink for atmospheric aerosol particles. "Dry deposition" by sedimentation and diffusion tends to be less important on global scales but is particularly relevant with respect to local air quality and health effects (inhalation and deposition in the respiratory tract). Depending on aerosol properties and meteorological conditions, the characteristic residence times (lifetimes) of aerosol particles in the atmosphere range from hours to weeks. After returning to the ground, viable bioparticles can continue biological reproduction and metabolic activity that may generate further emission of PBA particles and SOA precursors, thus closing a feedback loop and biogeochemical cycle of biologically-derived aerosols in the Earth system (Andreae and Crutzen, 1997; Deguillaume et al., 2008; Morris et al., 2014a; Pöhlker et al., 2012b; Pöschl, 2005; Pöschl et al., 2010; Suni et al., 2015).

In most terrestrial environments, bioaerosols constitute a substantial fraction of the atmospheric aerosol load (Tables 1a and 1b). With regard to number and mass concentration in the coarse particle size range with diameters larger than ~1 μm, bioaerosols typically account for around 30% in urban and rural air (Després et al., 2012; Huffman et al., 2013, 2010; Matthias-Maser and Jaenicke, 1995; Matthias-Maser et al., 2000a, 2000b; Monks et al., 2009; Schumacher et al., 2013; Sesartic et al., 2012) and up to ~80% in pristine rainforest air (Graham, 2003; Huffman et al., 2012; Martin et al., 2010; Pöhlker et al., 2012a; Pöschl et al., 2010). The number and mass concentrations of PBA particles over vegetated regions are typically in the order of ~10^4 m^{-3} and ~1 μg m^{-3}, respectively (Tables 1a and 1b; e.g., Bauer et al., 2002a, 2002b; Burrows et al., 2009a, 2009b; Després et al., 2012; Elbert et al., 2007; Heald and Spracklen, 2009; Huffman et al., 2013, 2012, 2010; Sesartic et al., 2012).

However, the actual identity, diversity, and abundance of different types of bioaerosol particles as well as their temporal and spatial

Table 1a
Estimates of global emissions and characteristic number and mass concentrations in near-surface air for different types of primary biological aerosol (PBA) particles.
Adapted from Després et al. (2012) and references therein.

	Global emissions [Tg a^{-1}]	Number concentration [# m^{-3}]	Mass concentration [μg m^{-3}]
Bacteria	0.4–28	~10^4	~0.1
Fungal spores	8–190	~10^3–10^4	~0.1–1
Fungal hyphal fragments		~10^3	
Pollen	47–84	~10 (up to ~10^3)	~1
Plant debris			~0.1–1
Algae		~100 (up to ~10^3)	~10^{-3}
Fern spores		~10 (up to ~10^3)	~1
Viral particles		~10^4	~10^{-3}
Total PBA	<10 (dominated by plant debris and fungal spores) to ~1000 (includes cellular fragments)		

variability are not well characterized. Recent studies suggest that the average number fluxes of emission of bacteria and fungal spores over continental regions are in the order of ~10^2 m^{-2} s^{-1} (Burrows et al., 2009a, 2009b; Crawford et al., 2014; Elbert et al., 2007; Heald and Spracklen, 2009; Lighthart and Shaffer, 1994; Lindemann et al., 1982; Sesartic and Dallafior, 2011), reflecting an intense and rapid exchange of biological matter and genetic information between atmosphere and biosphere. Estimates of global bioaerosol mass emission rates, however, vary widely (~10–1000 Tg a^{-1}; Tables 1a and 1b; Després et al., 2012), and the regional and temporal variations in the atmospheric abundance and fluxes of emission and transport of different types of bioaerosol particles are poorly constrained (Bowers et al., 2012, 2010, 2009; Burrows et al., 2009a, 2009b; Fröhlich-Nowoisky et al., 2012, 2009; Heald and Spracklen, 2009; Jaenicke, 2005; Sesartic and Dallafior, 2011).

Overall, the role of bioaerosols in the atmosphere and their interaction with terrestrial and marine ecosystems are not well described and understood – neither for the present state of the Earth system and climate, nor with regard to past evolution and future change. Indeed, the properties and interactions of atmospheric aerosols, including bioaerosols, are among the largest uncertainties in the current understanding and prediction of climate change (Solomon et al., 2007; Stocker et al., 2013). This lack of knowledge is particularly severe with regard to the assessment, prediction, and management of global environmental change in the Anthropocene as established by Paul Crutzen (Crutzen and Stoermer, 2000; Crutzen, 2002), i.e., in the present era of steeply increasing and globally pervasive human influence on the diversity, metabolic activity, and future development of life on planet Earth

Table 1b
Estimates of global emissions and mass burdens for different types of atmospheric aerosol components including organic carbon from primary biological aerosol (PBA) particles.
Adapted from Andreae and Rosenfeld (2008) and Monks et al. (2009).

	Global emissions [Tg a^{-1}]	Mass burden [Tg]
Carbonaceous aerosols		
Primary organic (0–2 μm)	95	1.2
Biogenic (PBA)	35	0.2
Biomass burning & fossil fuel	58	–
Black carbon (0–2 μm)	10	0.1
Secondary organic	28	0.8
Biogenic	25	0.7
Anthropogenic	3.5	0.08
Sulfates	200	2.8
Nitrates	18	0.49
Sea salt	10,130	15
Desert/soil dust	1600	18 ± 5
Anthropogenic total	312	3.1
Biogenic total	117	2.1

(Pöschl and Shiraiwa, 2015; Williams and Crutzen, 2013). For example, it is not clear how the ongoing global and regional changes in land use, climate, and biodiversity will affect the abundance and properties of atmospheric bioaerosols that may influence the spread of vegetation and disease as well as the spatial and temporal patterns of precipitation, which in turn may act as a positive or negative feedback on climate (Morris et al., 2014a). These issues are closely linked to societally relevant questions about how agriculture and other types of land use and human activity may be developed to efficiently mitigate or adapt to climate change. For example, these scenarios are more pertinent to the developing countries, especially densely populated South Asia, where information about bioaerosol properties and abundance is extremely limited.

In the following sections, this article will summarize the state of the science, highlight recent advances and outline future perspectives regarding bioaerosols and their role in the Earth system in terms of their identification and characterization, transport and transformation processes, as well as their interactions with climate, health, and terrestrial and marine ecosystems.

2. Identification and characterization of bioaerosols

A wide range of methods have been developed and applied for bioaerosol sampling and measurement: filter, impactor, impinger, and cyclone samplers; cultivation and staining techniques; immunological methods; light and electron microscopy; optical spectroscopy and mass spectrometry as well as chemical tracer analyses (Baron and Willeke, 2001; Buters et al., 2012; Carestia et al., 2015; Caruana, 2011; Cox and Wathes, 1995; Crook and Sherwood-Higham, 1997; De Linares et al., 2014; DeCosemo et al., 1992; Després et al., 2012; Georgakopoulos et al., 2009; Ghosh et al., 2015; Griffin et al., 2001; Griffiths and DeCosemo, 1994; Griffiths et al., 1997; Grinshpun and Clark, 2005; Grinshpun et al., 2005; Henningson and Ahlberg, 1994; Laskin et al., 2016; Levetin, 2004; Miyajima et al., 2014; Oteros et al., 2015; Valsan et al., 2015; West et al., 2016; Wittmaack et al., 2005; Xu et al., 2011; and references therein). Most of this work has been presented in the review by Després et al. (2012); therefore we focus in this section on recent advances in the following areas: Analysis of ribonucleic acids (DNA/RNA); fluorescence detection, spectroscopy and microscopy; X-ray microscopy and spectroscopy; and online and single-particle mass spectrometry.

2.1. Biological characterization

Microbiology has experienced an especially strong transformation over the last few decades. Most microorganisms cannot be grown readily in pure culture, and earlier studies using traditional microbiological cultivation techniques covered only small percentages of the species present in the investigated samples and environments; e.g., ~1% of bacteria, according to Lewis (2009), and ~17% of fungi, according to Bridge and Spooner (2001). The entire spectrum of atmospheric microbial diversity, i.e., the atmospheric microbiome is now becoming accessible through recent developments and applications of DNA- and RNA-based methods (e.g., Boreson et al., 2004; Maron et al., 2005; Peccia and Hernandez, 2006; Radosevich et al., 2002).

The identity of bioaerosols can be determined by DNA sequencing. Many studies use the traditional Sanger sequencing approach, as this provides sequences that are long enough to identify individual genera or species by comparison with sequences available in online databases like the National Center for Biotechnology Information (NCBI; Boreson et al., 2004; Després et al., 2007; Fahlgren et al., 2011; Fierer et al., 2008; Fröhlich-Nowoisky et al., 2009, 2012, 2014; Huffman et al., 2013; Maron et al., 2005; Urbano et al., 2011).

The Sanger sequencing-based bioaerosol analysis is being slowly replaced by modern Next Generation Sequencing (NGS) technologies. In the past, the length of the sequences has often been a limiting factor for the identification to the species or genus level, as the reads were much shorter than sequences obtained by Sanger sequencing. Next Generation Sequencing technologies are continuously improving and are currently able to provide sequences longer than 400 bp (Schmidt et al., 2013; Sinclair et al., 2015). These technologies also allow the generation of millions of reads from air samples in order to analyze the genomics and transcriptomics (RNA analysis), and have been successfully used in several recent bioaerosol related studies (e.g., Be et al., 2013; Bertolini et al., 2013; Bowers et al., 2013, 2012, 2011, 2010, 2009; Cao et al., 2014; DeLeon-Rodriguez et al., 2013; Franzetti et al., 2011; Kraaijeveld et al., 2015; Seifried et al., 2015; Tringe et al., 2008; Womack et al., 2015; Yooseph et al., 2013). In particular, metagenomic approaches enable comprehensive determination of the diversity and metabolic potential of the organisms present in an aerosol sample. Metagenomic techniques also allow the characterization of airborne viral diversity and dynamics, as viruses are genetically highly variable and do not possess conserved genes, which makes amplicon-based applications challenging (Prussin et al., 2014; Whon et al., 2012).

Fig. 3A shows an overview of the global atmospheric distribution of fungal phyla derived from Sanger sequencing of air samples collected at a wide range of geographic locations. The species richness of *Basidiomycota* (BMC) vs. *Ascomycota* (AMC) exhibits distinct biogeographic patterns with higher BMC/AMC ratios in continental air compared to marine air (Fröhlich-Nowoisky et al., 2012; Womack et al., 2010). Fig. 3B shows the relative abundance of fungal phyla in various soils and in tropical rainforest air, contrasting the total and metabolically active fungi determined by NGS sequencing of DNA and RNA (Womack et al., 2015).

Although sequence data from NGS studies provide information of the relative abundance of specific taxa, calculated as the fraction or percentage of the sequences representing the taxa of interest to the total amount of sequences, taxon-specific quantitative polymerase chain reaction (PCR) is the most accurate reflection of absolute concentrations (Dannemiller et al., 2014; Georgakopoulos et al., 2009). Quantitative PCR (qPCR) has been successfully applied to air samples to quantify individual species, genera, or groups of fungi, bacteria, or archaea (Casabianca et al., 2013; DeLeon-Rodriguez et al., 2013; Fröhlich-Nowoisky et al., 2014; Lang-Yona et al., 2012, 2014; Lee et al., 2010; Müller-Germann et al., 2015; Schweigkofler et al., 2004; Zeng et al., 2004, 2006). A promising new method for bioaerosol quantification is the droplet digital PCR (ddPCR) technique (Hindson et al., 2011; Jones et al., 2014); it utilizes a water-oil emulsion system in which the sample is fractionated into thousands of nanoliter droplets to enable high-throughput digital PCR.

Preliminary estimates of total DNA concentrations of several nanogram per cubic meter in urban air suggest that the amount of DNA inhaled by human adults may be as high as ~0.1–1 μg per day, which corresponds to ~10^{14}–10^{15} bp and would be equivalent to as much biological information as ~10^{7}–10^{8} bacterial genomes or ~10^{4}–10^{5} human genomes (Després et al., 2007). Due to the variability of atmospheric aerosol composition and experimental difficulties in the quantitative extraction and measurement of the total DNA content of air filter samples, however, these preliminary estimates remain to be confirmed and further specified for different environments and conditions.

2.2. Chemical and physical characterization

Recently, several new microscopy techniques have been developed that bypass the resolution limit of optical microscopy (super-resolution technologies) and allow the precise localization of intracellular components (Best et al., 2013; Betzig et al., 2006; Cremer, 2012; Hell and Kroug, 1995). Moreover, fluorescence imaging and spectroscopy techniques have also made tremendous progress in recent years. Wavelength-dependent fluorescence emission spectra, recorded as a function of excitation wavelength, can be plotted as three-dimensional landscapes, referred to as an excitation-emission matrix

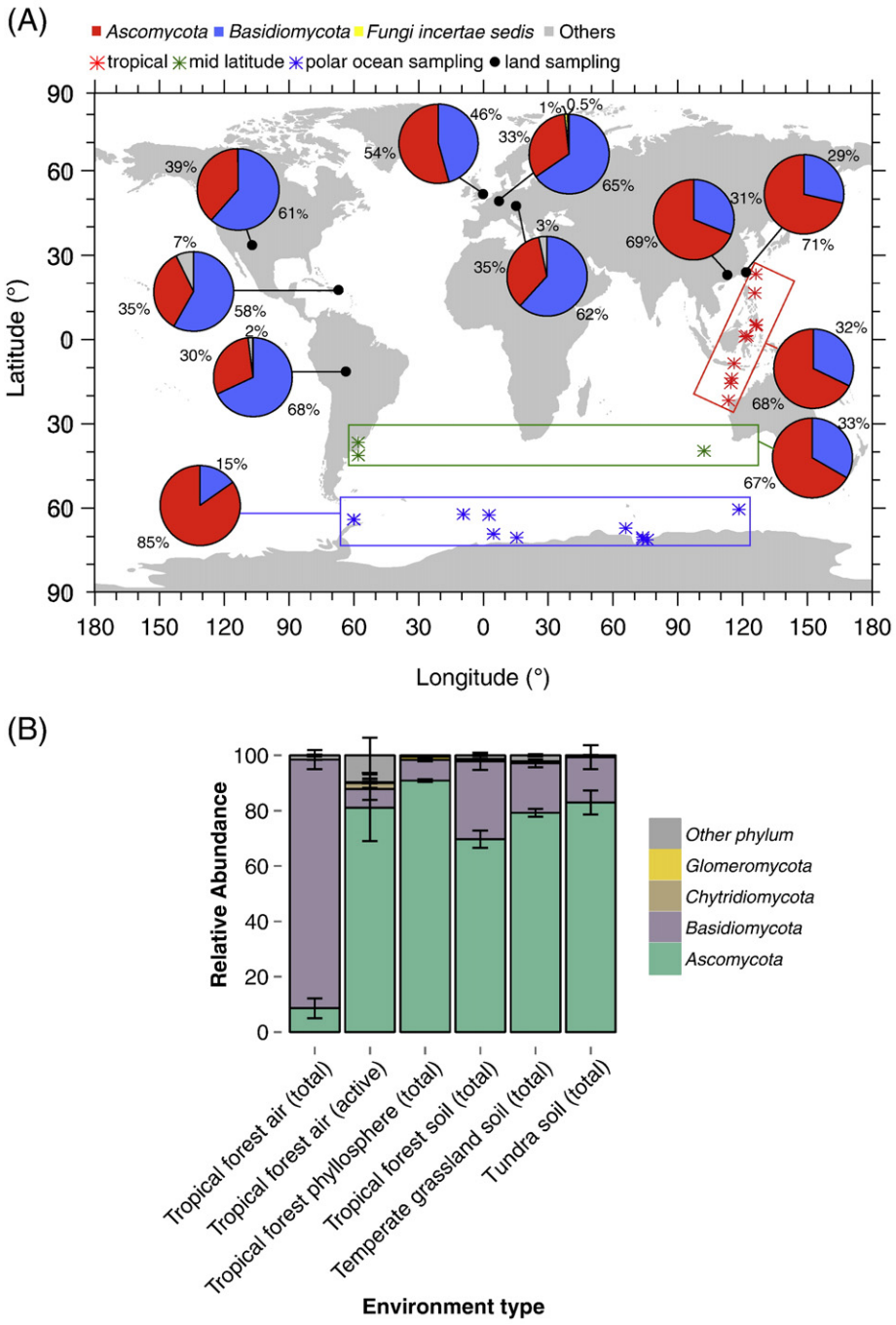

Fig. 3. Biodiversity and biogeography of airborne fungi determined by DNA and RNA analysis: (A) biogeography of airborne fungi over land and oceans: geographical location and relative proportions of different fungal phyla at continental, coastal, and marine sampling locations determined by Sanger sequencing and (B) relative abundances of fungal phyla in various soils and in tropical rainforest air, demonstrating differences in the composition of total and metabolically active airborne fungi determined by NGS sequencing of DNA and RNA (Womack et al., 2015).
(A) Adapted from Fröhlich-Nowoisky et al. (2012).

(EEM). Such plots, accordingly, relay a broad collection of information about the steady-state autofluorescence properties of a sample and can be regarded as a unique, sample-specific fingerprint. Fig. 4A displays a conceptual overview EEM, illustrating the spectral zones of interest, contour plots of three frequently investigated biological fluorophores (tryptophan, nicotinamide adenine dinucleotide phosphate [NADPH], and riboflavin), elastic scattering interferences, and operational ranges of selected fluorescence-detecting bioaerosol instruments (Pöhlker et al., 2012a). Fluorescence microscopy is well established and often used to study bioaerosols by taking advantage of either the autofluorescence of biological compounds or fluorescent stains specifically binding to various biological molecules. Fig. 4B and C shows fluorescence microscopy images of selected pollen species. Flow cytometry is also often employed to enumerate and characterize bioaerosols collected into water and then tagged with fluorescent stains (Chen and Li, 2005; Lange et al., 1997).

A number of instruments able to discriminate biological content in real-time based on the emission of laser/light-induced fluorescence (LIF) have been developed over the last two decades, originally for the rapid detection of biowarfare threat agents (Cheng, 1999; Crouzy

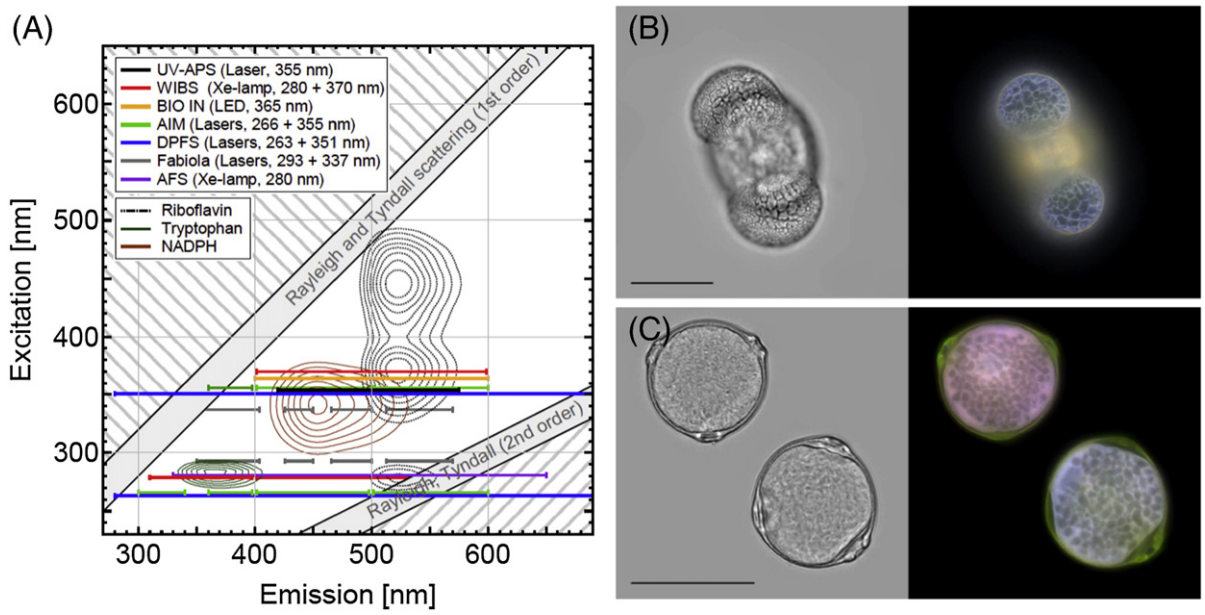

Fig. 4. Fluorescence spectroscopy and microscopy: (A) conceptual EEM displaying: fluorescence data area (white), areas strongly influenced by Rayleigh and Tyndall light scattering (grey diagonal bars), areas without meaningful data (grey stripes); contour lines for the fluorophores tryptophan, NADPH, and riboflavin; operational range of selected bioaerosol detectors represented by horizontal colored lines: UV-APS (ultraviolet aerodynamic particle sizer), WIBS (wideband integrated bioaerosol sensor), BIO IN (Bioaerosol single particle detector for the Fast Ice Nucleus CHamber (FINCH)), AIM (aerosol interrogation module), DPFS (Dual-excitation-wavelength Particle Fluorescence Spectrometer), Fabiola (Fluorescence Applied to BIOLogical Agents detection), and AFS (aerosol fluorescence sensor). Length of individual lines indicates measured emission band for a certain excitation wavelength shown as sharp line for purpose of clarity. Single-wavelength detectors are represented by one line, dual-wavelength detectors by two lines (Pöhlker et al., 2012a). High-resolution microscopy images of selected pollen species: (B) *Pinus sylvestris*, and (C) *Betula fontinalis* in bright field (left, scale bar = 30 μm.) and fluorescence mode (right). Fluorescence images shown as overlay of three channels (Pöhlker et al., 2013).

et al., 2016; Ho, 2002; Huffman et al., 2016; Kaye et al., 2000; Manninen et al., 2008; Pan et al., 2009; Pinnick et al., 1995; Sivaprakasam et al., 2004). Recently, several of these instruments have become commercially available and are among the most promising techniques for bioaerosol analysis (e.g., Agranovski et al., 2003; Brosseau et al., 2000; Hairston et al., 1997; Saari et al., 2014; Stanley et al., 2011). While these instruments do not offer the molecular specificity or detailed imaging capabilities of microscopy, many of them are able to provide an estimate of PBA properties in real-time, with high time and size resolution (Gabey et al., 2010; Healy et al., 2014; Huffman et al., 2010, 2012; O'Connor et al., 2014; Perring et al., 2015; Pöhlker et al., 2012a, 2013; Saari et al., 2015, 2016; Twohy et al., 2016; Ziemba et al., 2016).

Healy et al. (2014) compared measurements by two commercially available real-time instruments for characterization of bioaerosols using single particle fluorescence spectroscopy (wideband integrated aerosol sensor, WIBS-4, and ultraviolet aerodynamic particle sizer, UV-APS) with results from optical microscopy of Sporewatch single-stage impactor samples. As shown in Figs. 5 and 6, the different WIBS channels exhibited variable distributions, size-resolved diurnal concentrations, and correlations with fungal spore concentrations. The fluorescent particle number of the WIBS-4 channel FL3 and the UV-APS were strongly correlated and the particle size distribution was dominated by a 3 μm mode (Fig. 6). The diurnal plots show an increase in biological or fluorescent number concentration during the night and early morning hours, with daily minima occurring in the mid-afternoon, corresponding to the diurnal trend in relative humidity, which peaks at similar hours. Additionally, as displayed in Fig. 7, long-term UV-APS measurements at two climatically very different sampling sites, a boreal forest in Finland and a semi-arid site in Colorado, showed similar seasonal patterns with higher concentrations of fluorescent bioaerosols in summer (Manninen et al., 2014; Schumacher et al., 2013). Perring et al. (2015) used a WIBS-4 to detect fluorescent aerosol properties on a blimp transect across the whole of the southern United States, showing that number concentrations of fluorescent aerosol averaged up to 24% of the total aerosol number, with strong regional differences in number and size.

The use of fluorescence alone for detection of airborne biological particles is complicated by non-biological entities that exhibit fluorescence (e.g., certain SOA compounds, mineral dusts, and humic-like substances, HULIS) and by microorganisms that fluoresce too weakly to be detected by these techniques (Bones et al., 2010; Gabey et al., 2013; Huffman et al., 2010, 2012; Lee et al., 2013; Pinnick et al., 2004; Pöhlker et al., 2012a; Toprak and Schnaiter, 2013). Nonetheless, these limitations are minimized in pristine environments, where most of the ambient measurements to date have been recorded, and to a first approximation fluorescent bioaerosol particles (FBAP) can be considered as a lower limit for the abundance of biological particles (Huffman et al., 2010). Thus, time-resolved FBAP measurements contribute to improved parameterizations for daily, seasonal, and annual cycles to better reflect PBA emissions and effects in atmospheric modeling. Based on FBAP measurements at four locations in Europe, Hummel et al. (2015) incorporated a new parameterization into a regional model. Fig. 8A shows the FBAP emission fluxes (F_{FBAP}) simulated with this model for late August 2010, horizontally distributed over a model domain covering Europe. Averaged over the land areas of the domain, the mean F_{FBAP} is 1×10^3 m^{-2} s^{-1}. During July and October, the average fluxes are to 1.4×10^3 and 0.4×10^3 m^{-2} s^{-1}, respectively. The horizontally distributed near-surface (approximately 10 m above ground) FBAP/fungal spore number concentration using F_{FBAP} is shown in Fig. 8B.

Mass spectrometry (MS) is attractive for work in microbiology due to its speed (Krásný et al., 2013). Aerosol mass spectrometry can deliver single particle information to explore the spatial variability and dynamics of bioaerosols (Bozzetti et al., 2016; Chen et al., 2009; Fergenson et al., 2004; Kleefsman et al., 2007; Laskin et al., 2012; Pratt and Prather, 2012; Schneider et al., 2011; Tobias et al., 2005; van Wuijckhuijse et al., 2005). Another advantage of MS is that chemical tracer molecules, which are not easily accessible by sequencing or fluorescence labeling techniques, can be quantified on a single-particle basis

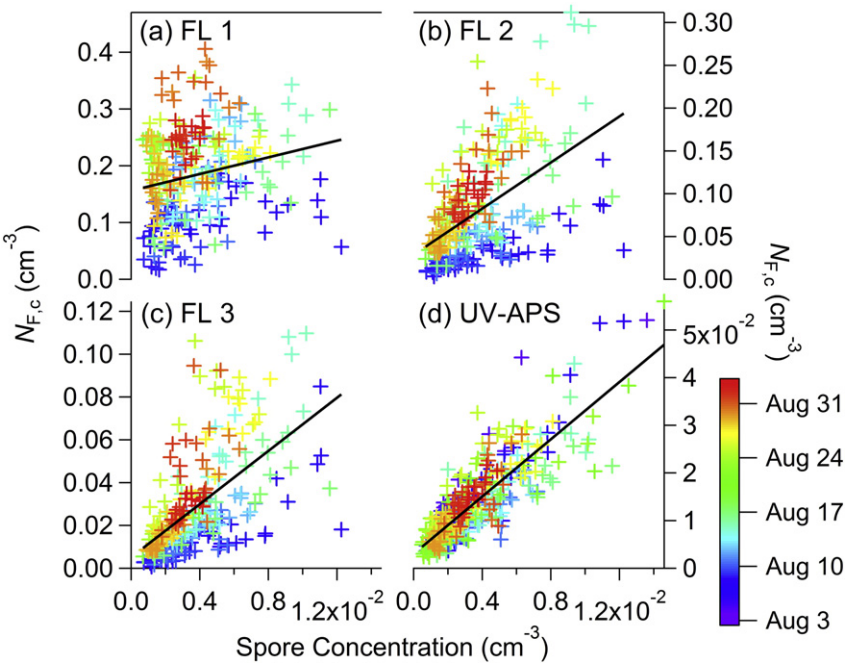

Fig. 5. Relationship of the mean fluorescent coarse particle concentration ($N_{F,C}$) determined by real-time instruments (WIBS-4 fluorescence channels FL1, FL2, and FL3; UV-APS) and spore concentrations from Sporewatch impactor sample analysis. Crosses represent 2 h measurement points, colored by sampling date. Black lines represent unweighted linear fits (Healy et al., 2014).

(e.g., lipids, cellulose, or biogenic SOA components; Buiarelli et al., 2013; Liang et al., 2013; Zhang et al., 2015). Recent developments in mass analyzer techniques, which combine high resolution with high mass accuracy (e.g., Orbitrap technology), are opening up new possibilities for biomarker and proteomic analyses (Hernàndez et al., 2012; Liu et al., 2016; Makarov and Scigelova, 2010; Pratt and Prather, 2012; Yates et al., 2009). Vibrational spectroscopy (infrared and Raman scattering) has also been utilized in a number of instances to characterize bioaerosols (Ben-David and Ren, 2003; Huston et al., 2004; Rösch et al., 2006; Thrush et al., 2012), and recently a Raman microscope for real-time analysis of bioaerosols has become commercially available (Ronningen et al., 2014).

Cell viability and vitality are other important aspects of bioaerosol analysis (Urbano et al., 2011). Viability, transformation, and adaptation are essential for the biological, ecological, and pathological roles of bioaerosols. Even bacterial ice nucleation has been suggested to be highly dependent on the status of cells, as proteins associated with intact cells have been proposed to be more efficient ice nuclei than purified proteins or proteins associated with disrupted cells (Möhler et al., 2007; Morris et al., 2004). Thus, in addition to the taxonomic and chemical identification of bioaerosols it is important to obtain information regarding their viability and metabolic activity to ascertain the role of bioaerosols in atmospheric processes.

Cultivation methods have long been used to detect living microorganisms. As pointed out above, only a small fraction of all species that exist in nature can be grown in the laboratory with the current culturing techniques. Thus, culturing can be particularly useful for targeting individual species or groups where culture conditions are known. In addition to culturing, bioluminescence-based techniques that detect the presence of adenosine-5′-triphosphate (ATP), the primary source of

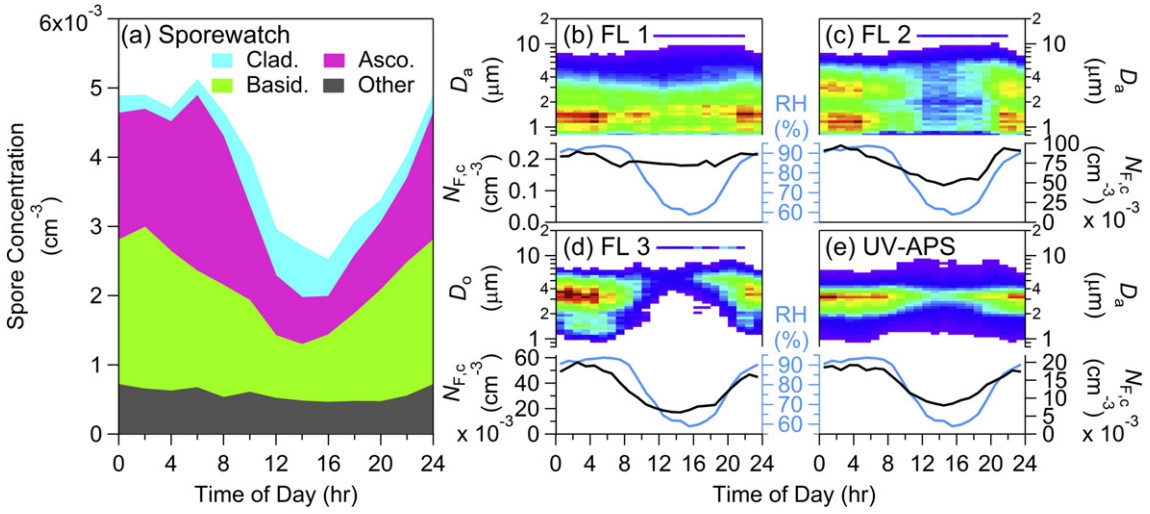

Fig. 6. Diurnal plots of spore number concentrations (a) and size-resolved number concentrations of fluorescent particles (upper half of panels b–e) and integrated fluorescent particle number ($N_{F,c}$, D_a > 1 µm) as the black trace and relative humidity as the blue trace (lower half of panel b–e) (Healy et al., 2014).

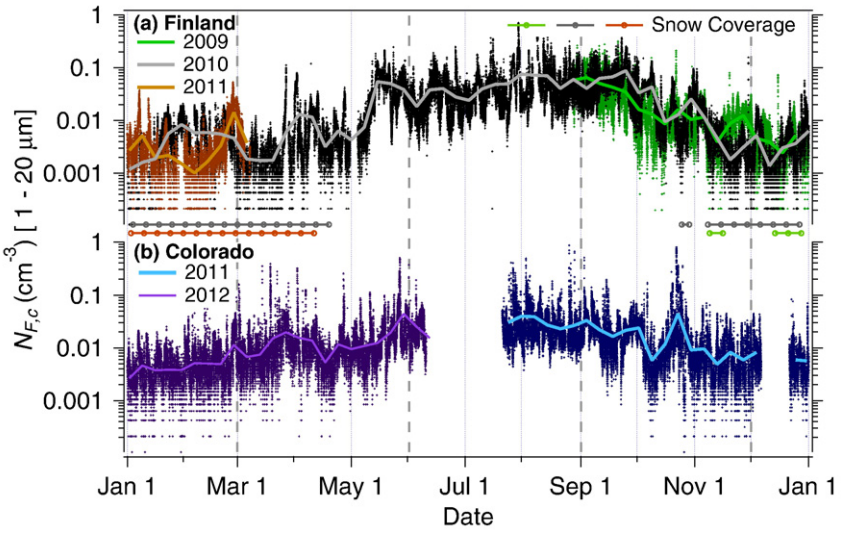

Fig. 7. Seasonal cycles of FBAP concentration measurements with the UV-APS at two climatically different sampling sites and key meteorological data (Schumacher et al., 2013).

energy in a living cell, allow a rapid but not species-specific assessment of the viable microorganisms in air and cloud water samples (Amato et al., 2007b; Lin et al., 2013; Park et al., 2014, 2015; Stewart et al., 1997; Stopa et al., 1999).

In summary, to gain a better understanding of the abundance, sources, transport, and transformation of bioaerosols, it is crucial to determine their chemical, genetic, and taxonomic composition as well as their concentration, seasonal variation, vitality, regional diversity, and evolution. Sophisticated techniques in the field of instrumental trace analysis (e.g., mass spectrometry) and microbiology, especially DNA sequencing technologies, need to be further developed and applied. Molecular probes for strain- to phyla-specific classification of microorganisms are necessary to open up new possibilities for the study of biological particles in the atmosphere. Metagenomic and metatranscriptomic analyses may prove especially useful to open a window on health-related issues, as the identity and activity of pathogens can be determined. The comprehensive characterization and identification of airborne microbial communities will impact various disciplines, including studies of microbial diversity and biogeography, public health, and microbial roles in biogeochemical cycling and climate processes.

3. Transport and transformation of bioaerosols

Since bioaerosols are released at the Earth's surface, they are typically most abundant in the lowest part of the atmosphere, the so-called

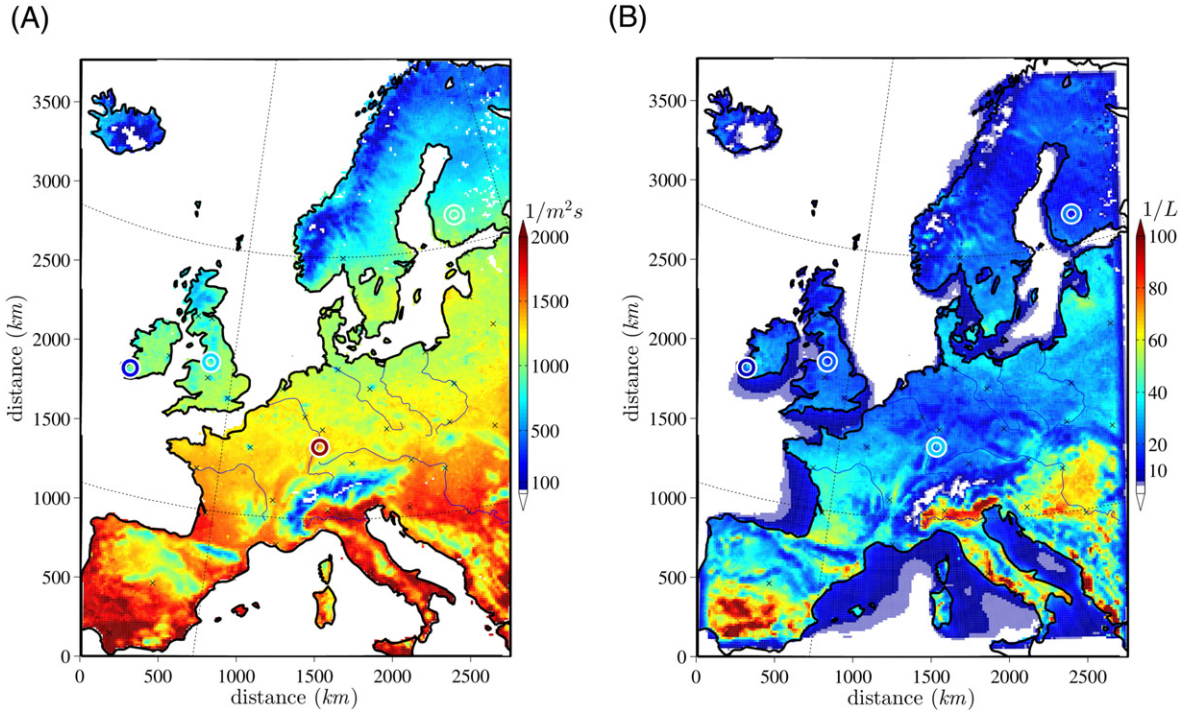

Fig. 8. Regional scale simulations: (A) average simulated FBAP emission flux (F_{FBAP}) in late August 2010 [m^{-2} s^{-1}] and (B) averaged horizontally distributed FBAP/fungal spore concentration, emitted by F_{FBAP}, in the lowest model layer, in late August 2010 [L^{-1}]. Circles indicate the locations of the different FBAP measurement time series and the color within the white circles represents the mean emission flux calculated from FBAP measurements at each location (Hummel et al., 2015).

planetary boundary layer (PBL). From a biological perspective it is particularly important to understand the transport processes in the PBL, since these transport processes affect the spread and the distribution of organisms and species, the speed of evolution, the formation of new species and microbial communities, and the adaptation to changing environmental conditions (Fröhlich-Nowoisky et al., 2012; Morris et al., 2014b; Womack et al., 2010). In atmospheric processes, bioaerosols play a role in the formation of cloud droplets, ice crystals, and precipitation, and may thus affect the hydrological cycle as well as atmospheric chemistry and physics (Amato et al., 2007a; Deguillaume et al., 2008; Diehl and Wurzler, 2010; Diehl et al., 2001; Hoose and Möhler, 2012; Huffman et al., 2013; Möhler et al., 2007; Morris et al., 2014a; Pöschl et al., 2010; Pratt et al., 2009; Prenni et al., 2009, 2013; Sesartic et al., 2012; Tobo et al., 2013). However, current knowledge on the vertical distribution of bioaerosols and the factors controlling their atmospheric transport over large scales and above the PBL based on observations is limited (Després et al., 2012).

3.1. Emission and transport

Global and regional models have been used to improve the scientific understanding of bioaerosol emission, transport, and atmospheric impact (Fig. 9; Ansari et al., 2015; Burrows et al., 2009a, 2009b, 2013b; Heald and Spracklen, 2009; Hoose et al., 2010; Hummel et al., 2015; Sesartic et al., 2012; Spracklen and Heald, 2014). These models are highly dependent on the correct representation of the emissions and the particle properties and modifications that might occur during transport, as well as on the correct representation of the small-scale transport processes themselves. Furthermore, these models do not address the biological consequences for the organisms concerning survival, vitality, and metabolic activity. Emission estimates of PBA particles suffer from large uncertainties (Elbert et al., 2007), which can range from 80 to 870% (Burrows et al., 2009a, 2009b). These uncertainties originate from biological processes in the ecosystems, including seasonality, life cycles, land cover changes, climatic dependencies, variation in microbial populations, and species competition. In addition, alterations caused by aging, chemical processing, and microphysics introduce additional challenges to estimating correctly global transport and effects of bioaerosols in the atmosphere (Burrows et al., 2013b). The emission strengths of bioaerosols and their interaction with atmospheric transport processes thus need improved quantification.

Close to the ground, turbulent small-scale transport drives the distribution of all particles emitted from the Earth's surface. The planetary boundary layer is directly affected by emissions from the surface and therefore also by the emission of bioaerosols. Depending on the geographic location and season, the thickness of the boundary layer undergoes a diurnal cycle, typically spanning a few hundred meters during nighttime, but extending up to 3 km during daytime. Diurnal and seasonal cycles of solar radiation and temperature stimulate biological activity, thereby constituting a strong link between biological activity, emissions, and atmospheric transport (Jones and Harrison, 2004; Matthias-Maser et al., 1995; Toprak and Schnaiter, 2013). Small-scale atmospheric processes, such as cloud processing in low-level clouds and wet deposition, further affect the abundance of bioaerosols in the atmosphere (Huffman et al., 2013). These atmospheric processes partly limit the travel distances in the boundary layer and reduce the number concentrations of non-biological as well as biological particles entering the free troposphere above the boundary layer (Sesartic et al., 2012). However, several processes like frontal uplift, convection, or turbulence at the boundary layer top may lead to an uplift of these air masses across the inversion capping the boundary layer into the free troposphere, where biological particles can potentially travel large distances as part of the tropospheric flow.

Direct measurements of bioaerosol abundance are mainly ground based. Even observations at 50 m above ground level are very sparse and only few measurements from aircraft (Andreeva et al., 2002; DeLeon-Rodriguez et al., 2013; Fulton, 1966; Gruber et al., 1998; Kourtev et al., 2011; Ziemba et al., 2016; Zweifel et al., 2012) or high altitude stations are available (Crawford et al., 2016; Gabey et al., 2013; Hallar et al., 2011; Matthias-Maser et al., 2000c). Consequently, global and regional model estimates regarding possible effects of bioaerosols on atmospheric processes also suffer from these uncertainties and need to be better constrained by observations in the atmosphere. Notably, knowledge of bioaerosol emission quantities close to their sources and of subsequent transformation processes is crucial for reliable estimations of the effects of bioaerosols on the atmosphere.

Estimates of emissions based on measurements of particle concentration also suffer from inherent uncertainties, as the removal rates of

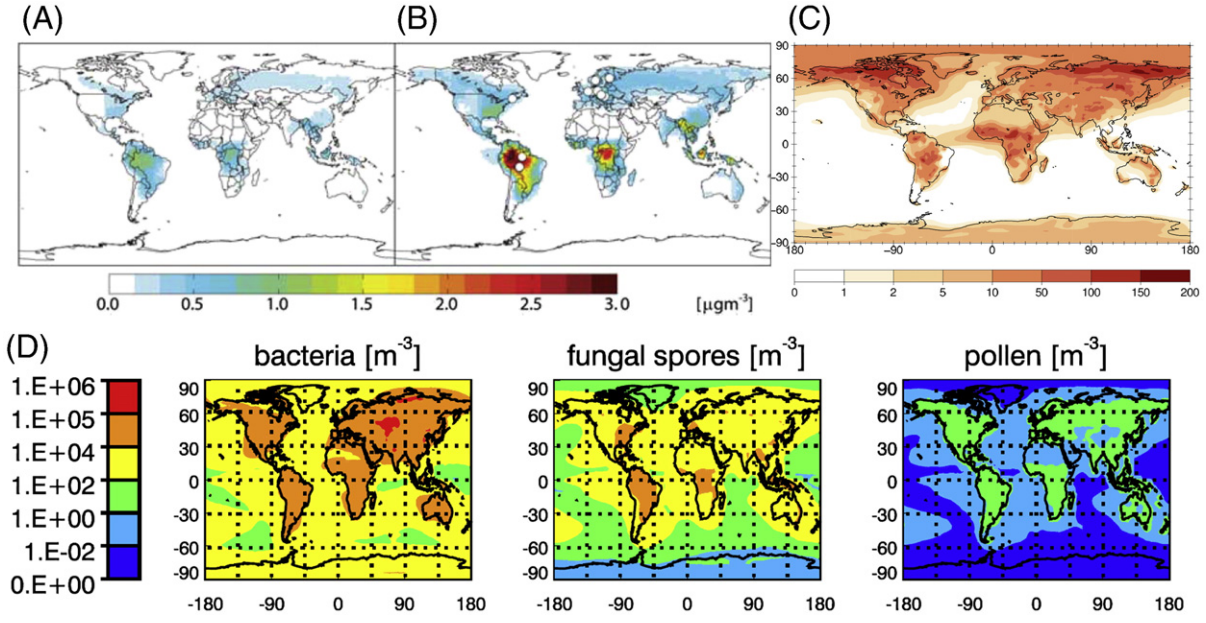

Fig. 9. Model results for annual-mean near-surface concentrations of PBA: (A) fungi in fine mode aerosol [µg m^{-3}], (B) fungi in coarse mode aerosol [µg m^{-3}], and (C) number of bacteria tracers [10^3 m^{-3}] (Burrows et al., 2009a, 2009b), (D) bacteria, fungal spores, and pollen [m^{-3}] (Hoose et al., 2010).
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particles from the atmosphere are not known and emissions must be inferred indirectly using models or assumptions about emissions. Measurements of bioaerosol emission fluxes by more direct methods, while less commonly performed, can provide valuable direct observational constraints. Possible methods for bioaerosol emission flux measurements fall into two general classes, gradient methods and eddy covariance-like methods. Gradient methods, such as the Bowen ratio method assume that the transport of atmospheric trace constituents in the boundary layer can be assumed to be analogous to the transport of more readily measureable quantities, such as heat and moisture. The Bowen ratio method and related gradient methods have been applied in many of the existing studies including direct flux measurements of bacteria and other bioaerosols (e.g., Crawford et al., 2014; Lighthart and Shaffer, 1994). These methods require a large number of measurements for statistical significance and suffer from inherent uncertainties due to the assumptions used to interpret the gradients.

Eddy covariance and related methods involve calculating the correlations between high-frequency time-series measurements of particulate or trace gas concentrations and the vertical wind speed. The eddy covariance method is regarded as the "gold standard" for flux measurements of trace gases and aerosol number fluxes (e.g., Gallagher et al., 1997; Norris et al., 2008; Pryor et al., 2007). This method requires fast-response instrumentation (typically 10 Hz or faster) and sufficiently high concentrations for robust statistical analyses, which are difficult to achieve for bioaerosols. In the absence of high-time-resolution measurement capabilities, an adaptation of eddy covariance known as "relaxed eddy accumulation" (Businger and Oncley, 1990; Gaman et al., 2004; Held et al., 2003, 2008), may be a more appropriate method for the measurement of bioaerosol fluxes. Relaxed eddy accumulation is based on conditional sampling of updrafts and downdrafts, and can be used with analysis methods that have much slower response times.

3.2. Physical, chemical, and biological transformation

The atmosphere not only acts as a passive transport medium, but also modifies the microphysical and chemical properties of living and dead biological matter. Cellular responses are initiated in living matter, whereas dead matter can be decomposed and become a source of cellular structures and smaller chemical compounds, which may influence the physical, chemical, and biological properties of the aerosols. Bioaerosol particles can undergo fragmentation in the atmosphere, and bioparticle fragments can be suspended from the Earth's surface into the air. Altering the size distribution and other properties of bioaerosol particles (surface and bulk composition, hygroscopicity, etc.) in turn can affect their ability to act as cloud condensation nuclei (CCN) or ice nuclei (IN), thus influencing their atmospheric transport and processing (Diehl et al., 2001; Morris et al., 2004; Schnell and Vali, 1972). Heterogeneous and multiphase chemical reactions can lead to oxidation, nitration, oligomerization, and degradation of proteins and other primary biological substances, modifying the molecular composition and biological activity of bioparticles. For example, reactions with air pollutants (e.g., O_3 and NO_2) have been shown to enhance the allergenic potential of airborne allergens, such as birch pollen, ragweed pollen, and *Aspergillus* spores (Franze et al., 2005; Gruijthuijsen et al., 2006; Lang-Yona et al., 2016; Reinmuth-Selzle et al., 2014; Zhao et al., 2016). Also, secondary organic and inorganic material can form a liquid or solid coating on bioparticles influencing their chemical, physical, and biological properties.

Certain types of bioparticles were specifically shaped by evolution to be transported by wind and use the atmosphere for their dispersal. These comprise endo- or resting spores of bacteria, fungi, mosses and ferns, pollen grains, and small plant seeds. These structures are generally found to have, on the one hand, thick cell walls sheltering them effectively from environmental stresses and, on the other hand, a minimal metabolism rate. These dispersal units are either actively emitted, such as wet-discharged fungal spores, or passively emitted, such as dry-discharged fungal spores, small seeds, and most pollen (Arditti and Ghani, 2000; Elbert et al., 2007; Jones and Harrison, 2004; Marshall and Chalmers, 1997; Morris et al., 2014b; Murren and Ellison, 1998). Besides such dedicated dispersal units, many other organisms, such as algae, (cyano)bacteria, fungi, and viruses, can also become aerosolized and are transported passively through the air. The vitality of these organisms is dependent on their adaptation or ability to react actively to changing environmental conditions (resilience). Moreover, also aggregation of cells, attachment to other aerosol particles, or protective envelopes may influence viability of bioaerosols (Amato et al., 2015; Morawska, 2006; Tong and Lighthart, 1998). However, although the atmosphere is intensively discussed as a possible habitat, hardly any studies exist that reveal the metabolic activity of microorganisms during their residence time in the atmosphere. Up to now, metabolic activity has been shown almost exclusively in specific small-scale environments like cloud droplets (Amato et al., 2005, 2007a, 2007b; Dimmick et al., 1975; Vaïtilingom et al., 2013).

The stresses induced in microorganisms while airborne influence their activity and vitality and thus their capability to colonize new habitats and to survive. Atmospheric stress can be considered an evolutionary force exposing airborne bioaerosols to selection pressure, thereby affecting the dispersal and evolution of microorganisms. Among the most significant stress factors are temperature, humidity, oxidative stress, starvation, radiation, and osmotic stress. Furthermore, it is believed that phylogenetic aspects of primary biological particles in the atmosphere lead to a selection of species becoming airborne or transported as living matter to high altitudes (Alfreider et al., 1996). How airborne transport affects different microorganisms and their ability to settle and then proliferate again is currently not well understood.

3.3. Cloud interactions and bioprecipitation cycle

The role of biological particles in cloud formation, precipitation, ecosystem interactions, and possible feedback cycles is a topic of increasing interest (Amato et al., 2015; Andreae and Rosenfeld, 2008; Ariya et al., 2009; Ariya and Amyot, 2004; Després et al., 2012; Haga et al., 2013; Hoose and Möhler, 2012; Huffman et al., 2013; Joly et al., 2014; Mason et al., 2015; Michaud et al., 2014; Möhler et al., 2007; Morris et al., 2014a; Pöschl et al., 2010; Pratt et al., 2009; Sands et al., 1982; Stopelli et al., 2015; and references therein). For plant pollen and many microorganisms aerial dispersal is part of their life cycle (Brown and Hovmøller, 2002). To maintain viability in the atmosphere, microorganisms have adapted to the conditions in the atmosphere and evolved survival strategies for long-distance dispersal or dispersal at high altitudes (Griffin, 2004; Imshenetsky et al., 1978; Joly et al., 2015; Kellogg and Griffin, 2006; Morris et al., 2011; Prospero et al., 2005; Womack et al., 2010).

As already mentioned above, microorganisms and other bioaerosols are removed from the atmosphere either by dry or wet deposition, i.e., incorporation into cloud droplets or ice crystals, possibly influencing precipitation, the hydrological cycle, and climate (Fig. 2). Biological CCN or IN may be present as living or dead cells, cell fragments, hyphae, pollen, spores, detached IN-active macromolecules, biogenic potassium-salt particles, or associated with plant particles or soil organic matter (e.g., Bauer et al., 2003; Conen et al., 2011; Després et al., 2012; Diehl et al., 2001; Dingle, 1966; Franc and Demott, 1998; Fröhlich-Nowoisky et al., 2015; Hill et al., 2016; Hiranuma et al., 2015; Huffman et al., 2013; Kieft and Ahmadjian, 1989; Kieft, 1988; Maki and Willoughby, 1978; Möhler et al., 2007; O'Sullivan et al., 2016; Pöhlker et al., 2012b; Pouleur et al., 1992; Pummer et al., 2012, 2015; Šantl-Temkiv et al., 2015; Sattler et al., 2001; Schnell and Vali, 1976; Schnell and Vali, 1972; Tobo et al., 2014; Vali et al., 1976).

Cloud condensation nuclei can nucleate liquid cloud droplets. The potential for a particle to act as CCN is ranked by the atmospheric water vapor pressure required for it to nucleate and depends on both its size and composition (Andreae and Rosenfeld, 2008; Farmer et al., 2015). Some pollen, fungal spores, and bacteria can be activated as

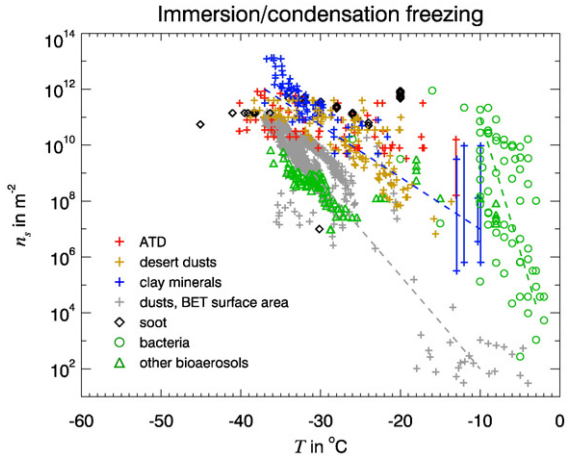

Fig. 10. Ice-nucleation-active site densities for Arizona test dust (ATD), kaolinite, natural desert dusts, soot, and bioaerosols for immersion freezing, including deposition, and condensation freezing experiments at or above water saturation. The lines are inserted to guide the eye. The blue line refers to ATD, desert dusts, and clay minerals. The green line refers to biological aerosols (Hoose and Möhler, 2012).

CCN at relatively low supersaturation levels and are called giant CCN due to their large size compared to other non-bioaerosol CCN-active aerosols (e.g., Andreae and Rosenfeld, 2008; Bauer et al., 2003; Delort et al., 2010; Franc and Demott, 1998; Hassett et al., 2015; Pope, 2010; Sun and Ariya, 2006). For example, Bauer et al. (2003) isolated several bacterial species from aerosol and cloud water samples that were activated as CCN at supersaturations between ~0.07 and 0.11%. In the atmosphere, giant CCN represent a small fraction (0.001–0.01%) of particles (Posselt and Lohmann, 2008). Nevertheless, they are of special interest, because they will be activated first, grow readily and play a role in shaping cloud cycles (Andreae and Rosenfeld, 2008). According to a global modeling study, the incorporation of the giant CCN accelerates the hydrological cycle, so that clouds precipitate faster (but not more) and less condensed water is accumulated in the atmosphere (Posselt and Lohmann, 2008). Additionally, it has been shown that pollen grains can rupture under humid conditions and release cytoplasmic material, forming submicron particles that can act as CCN (Steiner et al., 2015; Taylor et al., 2002, 2004).

Ice particles in the atmosphere can be formed via homogeneous or heterogeneous ice nucleation. Homogeneous freezing of liquid water droplets is a time-dependent stochastic process, which can be described by the formation of an ice embryo with critical size, whose probability to form ice increases with time (Pruppacher and Klett, 2010). In contrast, heterogeneous freezing is triggered by foreign particles or macromolecules serving as IN (Hoose and Möhler, 2012; Pummer et al., 2015).

Bioaerosols had already been found in ice crystals in the late 1950s (Ariya and Amyot, 2004; Schnell and Vali, 1976; Vali et al., 1976). Fig. 10 shows that biological IN, such as bacteria, are much more efficient IN for immersion freezing than mineral dust or soot, as they can trigger ice formation at high subzero temperatures (Hoose and Möhler, 2012). Thus, biological IN can be expected to be important for clouds or cloud regions warmer than −15 °C (DeMott and Prenni, 2010; Morris et al., 2014a; Murray et al., 2012). Additionally, between

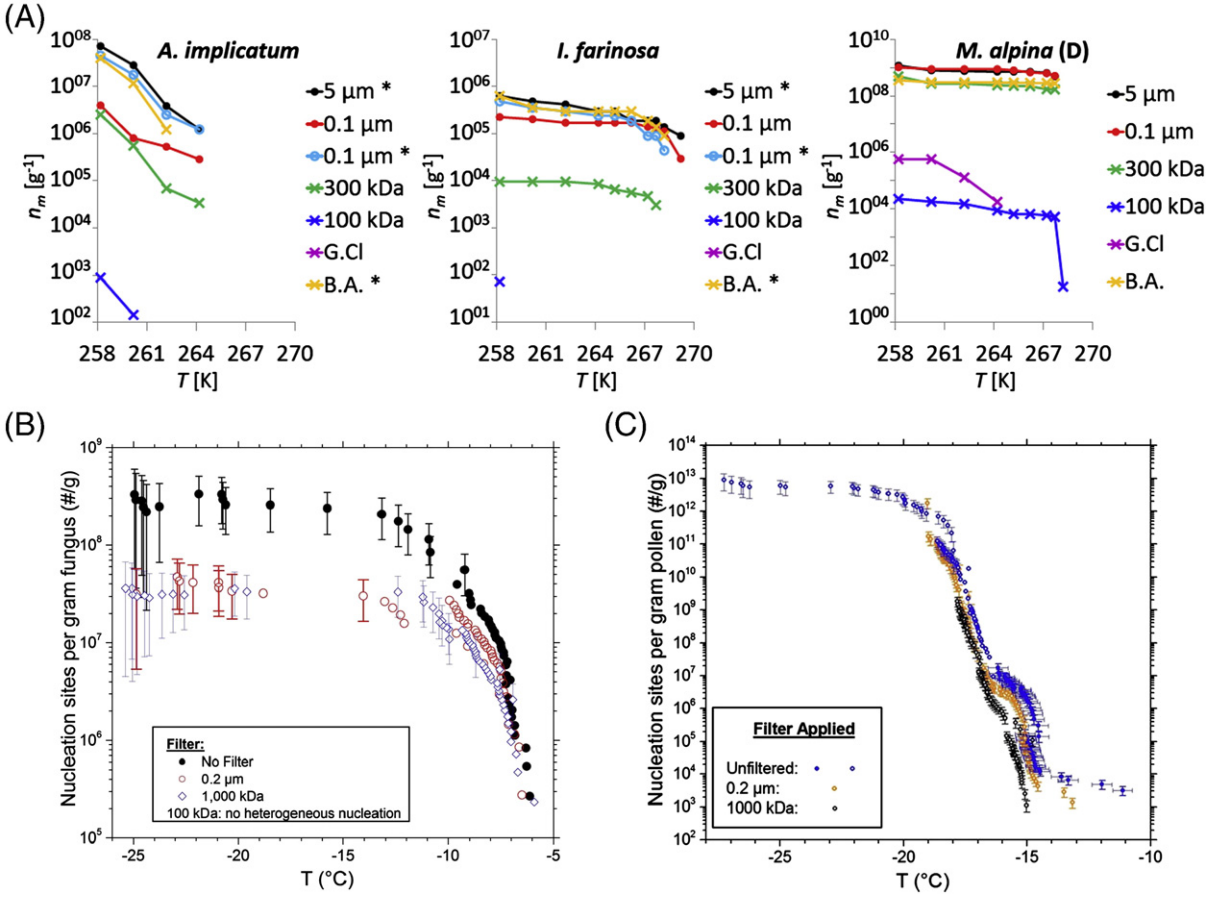

Fig. 11. Cumulative IN spectra before and after filtration for different fungal species and pollen: (A) *Acremonium implicatum* (now *Sarocladium implicatum*), *Isaria farinosa*, *Mortierella alpina* (Pummer et al., 2015), (B) *Fusarium avenaceum*, and (C) pollen from *Betula pendula* (O'Sullivan et al., 2015).

temperatures of −3 °C and −8 °C, ice multiplication by the Hallett-Mossop process might occur, leading to higher concentrations of ice crystals by rime splintering of ice particles (Hallett and Mossop, 1974).

The best studied IN-active microorganisms are bacteria, which have been found in the boundary layer and in the upper troposphere (Lindemann and Upper, 1985; Lindemann et al., 1982). Many strains of the genera *Pseudomonas*, *Pantoea*, and *Xanthomonas* are IN-active and express isoforms of the same IN-active protein (Hill et al., 2014a). The proteins are anchored in the outer membrane and can form large aggregates triggering ice nucleation at up to −1.5 °C (Kozloff et al., 1991; Lindow, 1989). As shown in Fig. 10, IN-active bacteria, such as some *Pseudomonas syringae* strains, reach IN-active surface site densities of $>10^{10}$ m^{-2} already at temperatures above −10 °C, whereas for mineral dust, these values are typically reached only below −20 °C. Recent investigation of the interaction of *P. syringae* with water molecules demonstrated that the IN-active protein enhances ice nucleation by arranging water molecules into alternating stripes of higher and lower-ordered molecules, and that latent heat is effectively removed from the nucleation site (Pandey et al., 2016).

Ice nucleation activity has also been documented in pollen, algae, fungi, lichen, insects, leaf litter, and plankton, as reviewed elsewhere (Després et al., 2012; Moffett et al., 2015; Pummer et al., 2015; von Blohn et al., 2005). For example, laboratory experiments examining the IN activity of pollen in the immersion mode have shown that birch pollen grains can induce freezing of droplets at temperatures as high as −9 °C (Diehl et al., 2002). Recently, IN activity has been discovered in several moss and liverwort species (Moffett, 2015; Weber, 2015). Moreover, Mortazavi et al. (2015) isolated an IN-active bacterium possibly belonging to the genus *Bacillus* (96% similarity) from fresh snow. There is also a growing interest in the IN properties of fungal species, and IN activity above −20 °C has been found in several fungal species, such as *Boletus zelleri* (Haga et al., 2014), *Endocronartium harknessii* (Haga et al., 2013), *Hemileia vastatrix* (Morris et al., 2013), *Isaria farinosa* (Huffman et al., 2013), *Mortierella alpina* (Fröhlich-Nowoisky et al., 2015), *Puccinia* spp. (Haga et al., 2013; Morris et al., 2013), *Sarocladium* (formerly *Acremonium*) *implicatum* (Huffman et al., 2013), and *Ustilago nigra* (Haga et al., 2014).

Particularly interesting is the observation of detached nanometer-sized IN-active macromolecules (INM) that are active at high temperatures in fungal species of different phyla and in pollen (Fig. 11; Fröhlich-Nowoisky et al., 2015; O'Sullivan et al., 2015; Pouleur et al., 1992; Pummer et al., 2012, 2015). Associated with soil dust particles, these INM may impact cloud glaciation indirectly, indicating a higher contribution and importance of biological, in particular fungal, IN than previously assumed (Fröhlich-Nowoisky et al., 2015; O'Sullivan et al., 2015; Pummer et al., 2015). For proteinaceous INM from *Fusarium avenaceum* it was recently demonstrated that they can be adsorbed onto kaolinite, a common soil clay mineral, conferring their IN activity to the mineral particles (O'Sullivan et al., 2016). Augustin-Bauditz et al. (2016) presented similar findings of illite-NX particles mixed with birch pollen INM. Moreover, nanometer-sized particles of biological and inorganic origin were found to be the most abundant particles in snow samples from different ecosystems (Rangel-Alvarado et al., 2015).

It is still an open question whether there are sufficient numbers of CCN- and IN-active bioaerosols at cloud altitudes to affect cloud formation and evolution. However, in pristine air over vegetated regions or under remote conditions, bioaerosols might represent a significant fraction of CCN and IN and are likely to be an essential regulating factor in the formation of clouds and precipitation (Andreae and Rosenfeld, 2008; Healy et al., 2014; Huffman et al., 2013; Pöhlker et al., 2012b;

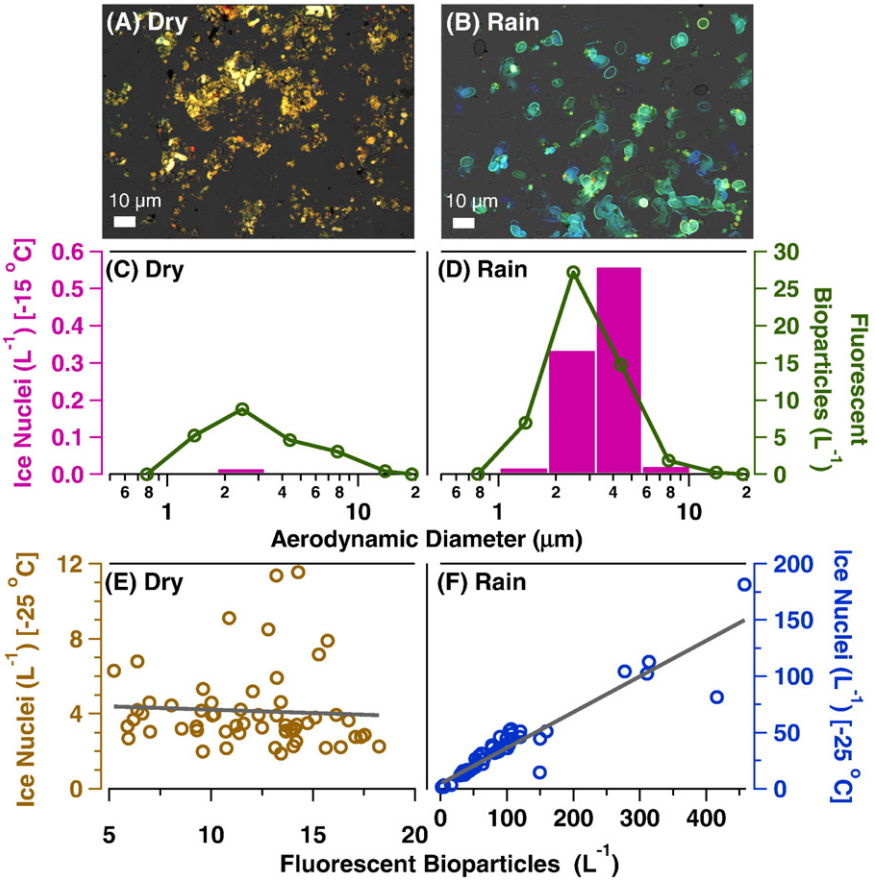

Fig. 12. Aerosol properties during dry periods and rain events: (A, B) fluorescence microscope images of aerosol impactor samples, (C, D) size distributions of IN and of fluorescent bioparticles, and (E, F) number concentrations of IN plotted against fluorescent bioparticles (Huffman et al., 2013).

Pöschl et al., 2010). Moreover, Creamean et al. (2013) found by direct cloud and precipitation measurements that long-range transported dust mixed with biological residues plays an important role in cloud ice formation and precipitation processes over the western United States. Wright et al. (2014) proposed that increasing relative humidity, due to a cold-frontal passage, could trigger the release of biological IN, which in turn may seed the frontal cloud band. Increasing concentrations of bioaerosols and IN during and after rain events have been found in a forest ecosystem (Fig. 12; Huffman et al., 2013; Prenni et al., 2013; Tobo et al., 2013).

Fig. 12A and B shows microscopic images of aerosol impactor samples highlighting the contrast between irregularly shaped dust in a sample collected during dry weather and cellular structures in a sample collected during a rain event. During dry weather conditions dominated by dust, the concentrations of IN at −15 °C were between 0.01 and 0.02 L^{-1}, and no correlation with FBAP concentration was found (Fig. 12C and E). In contrast, during rain events, the size distribution of IN exhibits a distinct peak in the range of 2–6 μm that coincides with the peak of the size distribution of FBAP (Fig. 12D). Furthermore, the measured IN concentrations followed a close linear correlation with FBAP concentration (Fig. 12F). The strong contrast between dry and rainy periods suggests that the release of PBA during and after rain may play an important role in the spread and reproduction of microorganisms in certain environments, and it may also contribute to the atmospheric transmission of pathogenic and allergenic agents (Fig. 13A; Huffman et al., 2013).

Additionally, long-term measurements of IN concentrations and rainfall in Australia indicate strong links between microorganisms and rainfall that persist over longer periods of time than previously assumed (Bigg et al., 2015). Ice nucleation activity that promotes the formation of precipitation would be a beneficial adaptation for microorganisms to return to the land surface under favorable conditions (Fig. 13; Morris et al., 2008; Sands et al., 1982). A feedback cycle involving the release of plant-associated microorganisms that are transported to cloud altitudes, followed by microbial rainfall induction resulting in increased plant and microbial growth, was already proposed in 1982 (Sands et al., 1982). This bioprecipitation feedback mechanism and related biotic processes involved in the hydrological cycle may have played an important role in the coevolution of life and climate as well as in the future development of the Earth system in the course of the Anthropocene (Christner et al., 2008; Huffman et al., 2013; Morris et al., 2014a; Pöschl and Shiraiwa, 2015). A more detailed discussion linking the bioprecipitation feedback cycle with Earth history and biological species evolution is given in Morris et al. (2014a).

Primary biological aerosols also contribute to the abundance of IN in marine environments. Ice nucleation activity has been identified in several marine bacteria and phytoplankton species (Alpert et al., 2011a, 2011b; Knopf et al., 2010; Parker et al., 1985; Schnell and Vali, 1975; Schnell, 1975). As summarized in section 4.2, particulate matter of biological origin can be emitted via sea spray from marine sources. Organic matter from the sea-surface microlayer has been shown to be a source of atmospheric IN (Wilson et al., 2015), and laboratory simulations using real wave breaking in a laboratory flume showed an increase of sea spray IN emissions associated with phytoplankton blooms (DeMott et al., 2015).

Different model simulations suggest regional differences in the importance of marine biogenic IN (Burrows et al., 2013a; Wilson et al., 2015). As illustrated in Fig. 14, marine biogenic IN are likely to play a dominant role in the near-surface air in remote marine regions, such as over the Southern Ocean. These regions are less influenced by long-distance transport of continental dust and more affected by sea spray generation due to strong winds.

Climate and land-use related changes in the atmospheric abundance of bioaerosols and in consequence of biological CCN and IN could result in previously unconsidered feedbacks that influence the hydrological cycle and the Earth's energy balance (Andreae and Rosenfeld, 2008; Burrows et al., 2013a).

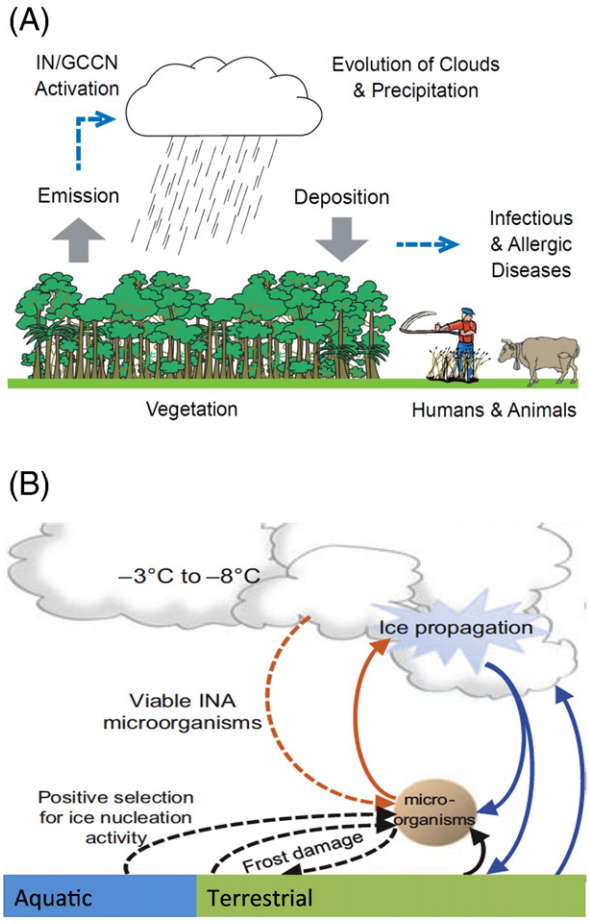

Fig. 13. Bioprecipitation cycle. Terrestrial ecosystems are the major source of ice nucleation active microorganisms; precipitation and humidity can enhance bioparticle emissions (rain splash, active wet discharge, etc.); bioparticles serving as ice nuclei or giant cloud condensation nuclei (IN/GCCN) can influence the evolution of clouds and precipitation, which provide water for growth of vegetation and for multiplication of microorganisms (A, B). Deposition of pathogenic and allergenic species can trigger human, animal and plant diseases (A; Huffman et al., 2013). Ice nucleation activity of microorganisms is positively selected in various ecosystems, on frost damaged plants and with precipitation itself. (B) Adapted from Morris et al. (2014a); copyright 2013, with permission from John Wiley and Sons, Inc.

Integration and synthesis of experimental studies, measurement data, and model calculations of bioparticle emission, transport, transformation, and deposition will be essential to achieve full understanding of the atmospheric lifecycle of bioaerosols and to find out if bioprecipitation and related effects are important for the co-evolution of climate and life on Earth.

4. Bioaerosol-ecosystem interactions

4.1. Terrestrial ecosystems

Terrestrial ecosystems are major sources of atmospheric bioaerosols. Vascular plants and fungi are well known to produce and release pollen and spores during reproduction, and fragments of plant and fungal tissues can also be emitted into the atmosphere in the course of decay processes (Després et al., 2012; Jaenicke, 2005; Matthias-Maser et al., 2000b). Less well-known emission sources of bioaerosols are microbial surface communities or cryptogamic covers consisting of (cyano)bacteria, archaea, algae, fungi, lichens, and bryophytes in varying proportions. As so-called cryptogamic ground covers they occur on soil and rocks, forming biological soil and rock crusts as

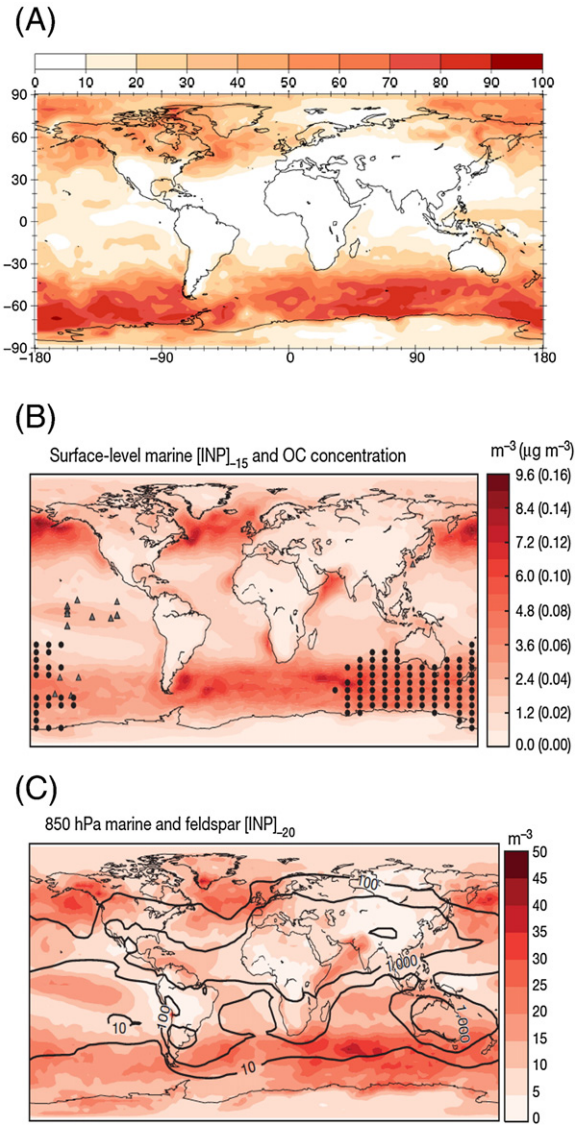

Fig. 14. Global model simulations of marine biogenic IN: (A) simulated annual mean relative contribution of marine biogenic IN to marine boundary layer IN concentrations at −15 °C, given in percent (Burrows et al., 2013a), (B) simulated distribution of IN (here displayed as ice nucleating particle (INP)) concentration active at −15 °C [m^{-3}] and surface-level marine aerosol organic mass concentration [µg m^{-3}], and (C) modeled distribution of marine biogenic IN concentrations active at −20 °C at 850 hPa (corresponding to the altitude of high-latitude mixed-phase clouds).
Images B and C reprinted with permission from Macmillan Publishers Ltd.: Nature. Wilson et al., 2015, copyright 2015.

well as bryophyte and lichen carpets. Cryptogamic plant covers spread over large portions of terrestrial plant surfaces, including stems, branches, and leaves of trees and shrubs (Fig. 15). These cryptogamic covers have been estimated to cover about one third of the available and suitable ground surface area (i.e., ~27.3×10^6 km^2) and one third of the suitable plant surface area (i.e., ~57.3×10^6 km^2; see Supplementary Table S1 in Elbert et al., 2012). Thus, cryptogamic covers have a total estimated projected surface area of ~85×10^6 km^2, being larger than the surface area of Africa and the Americas combined, and thereby contribute to the terrestrial bioaerosol formation. This also explains why microorganisms and bryophytes contribute large diversity and number concentrations per unit surface area in various natural and anthropogenically influenced environments (Hantsch et al., 2013; Lindow and Brandl, 2003; Morris and Kinkel, 2002; Yadav et al., 2005).

Plant pollen, fungal spores, bacteria, algae, and cyanobacteria have been identified in bioaerosol samples (e.g., Bauer et al., 2002a; Bowers et al., 2013; Brown et al., 1964; DeLeon-Rodriguez et al., 2013; Delort et al., 2010; Després et al., 2012; Favero-Longo et al., 2014; Fröhlich-Nowoisky et al., 2009; Marshall and Chalmers, 1997; Sesartic and Dallafior, 2011; Smets et al., 2016), but their interactions with different habitats have not been resolved. In addition, the relative importance of vascular plants and cryptogamic covers has not been investigated across different biomes and ecosystems. Plants and fungi also release volatile organic compounds (Kesselmeier et al., 1999; Wilske and Kesselmeier, 1999; Wilske et al., 2001) and have been proposed as a source of small (≤100 nm) potassium salt particles that can act as nuclei for the condensation of low-volatility organic vapors in rainforest air (Pöhlker et al., 2012b). Thus, both vascular plants and cryptogamic organisms can influence the composition, quantity, and chemical processing of bioaerosols. Apart from its role as a source of bioaerosols, vegetation is also affected by the deposition of bioaerosols from the atmosphere, influencing the dispersal, genetic mixing, and evolution of plants and microorganisms.

Both bioaerosol formation and the effects of bioaerosols on vegetation are influenced by climate and habitat conditions. Land use change is also known to affect the formation and dispersal of bioaerosols. Once natural lands are converted to human use (e.g., agriculture and construction), natural vegetation and cryptogamic covers are often destroyed. As biological soil crusts are well known to stabilize the soil surface, drastically reducing the erosive effects of wind (Belnap and Gillette, 1998; Eldridge and Leys, 2003), their destruction, besides the damage to vascular plant vegetation, causes increases in frequency and strength of dust storms, as for example experienced in the western United States during settlement in the 19th century (Neff et al., 2008). But also recent dust storm events, as in China, are considered to be largely caused by land use changes (Hill et al., 2014b). Soil dust particles containing biogenic compounds, which are also expected to be emitted during these events, have been described to be particularly potent during ice nucleation processes (e.g., Schnell and Vali, 1972; O'Sullivan et al., 2015). As the vitality of cryptogamic covers and organisms depends strongly on the availability of water in their environment, they are particularly susceptible to the bioprecipitation feedback mechanisms outlined above (Sect. 3.3). Thus, bioaerosol emissions from cryptogamic covers may be strongly affected by global change and should be further investigated and explicitly considered in regional and global models of atmosphere, biosphere, and climate interactions.

4.2. Aquatic ecosystems

Compared to terrestrial ecosystems, much less is known about the contribution of marine ecosystems as sources and sinks of bioaerosols, although oceans cover >70% of the Earth's surface. On one hand, bioaerosols over the oceans are influenced by terrestrial sources and long-distance transport of microbes, e.g., plant and human pathogens (Brown and Hovmøller, 2002; Cho and Hwang, 2011; Sharoni et al., 2015). On the other hand, the oceans themselves are sources of bioaerosols (Aller et al., 2005; Amato et al., 2007b; DeLeon-Rodriguez et al., 2013; Després et al., 2012; Fahlgren et al., 2015; Leck and Bigg, 2005; Matthias-Maser et al., 1999; Pósfai et al., 2003). Bacterial cell concentrations in marine and freshwater environments are around 10^6 mL^{-1}, whereas virus particle concentrations are larger, at around 10^7–10^{10} mL^{-1} (Cho and Hwang, 2011; Maranger and Bird, 1995; O'Dowd et al., 2015). These microbes can become airborne by the eruption of rising bubbles through the sea-surface microlayer as illustrated in Fig. 16 (Aller et al., 2005; Blanchard, 1975; Blanchard et al., 1981; Hultin et al., 2011; Veron, 2015; Wilson et al., 2015). Film and jet drops are generated behind the breaking wave crest when bubbles burst or when the bubble cavity collapses. Additionally, if the wind speed is high enough, spume drops can be ejected from the breaking wave crest (Veron, 2015). The bubble-bursting results in an enrichment of microbes in the aerosol compared to subsurface water (Aller et al., 2005; Wilson et al., 2015). Depending on the concentration of bacteria

Fig. 15. Cryptogamic covers (microbial surface communities) growing on rock, plants, and soil: (A) cryptogamic rock cover: mosaic of lichens on granitic rock, Cape Point, South Africa, (B) cryptogamic plant cover: epiphytic lichens (*Teloschistes capensis*), Cape Point, South Africa, and (C) biological soil crust dominated by the green-algal lichen *Psora decipiens*, Soebatsfontein, South Africa. All scales = 5 cm.

in the surface water and the enrichment factor, the estimated global emission of marine bacteria is between 2000 and 10,000 Gg a^{-1} (Burrows et al., 2009b). This estimate is based on a small number of measurements, as most measurements of airborne bacteria have focused on urban or rural locations. Furthermore, until recently, marine bioaerosol studies often relied on traditional culture-dependent techniques, thus detecting only the viable and culturable fraction of bacteria. The majority of the bacterial population remained undetected in these studies, as the culturability of seawater bacteria is estimated to be between 0.001% and 0.1% (Amann et al., 1995). For a more detailed discussion of the problem of culturability of airborne bacteria see Burrows et al. (2009b). Recently, some studies used a combination of culture-dependent and culture-independent methods such as cloning and DGGE (denaturing gradient gel electrophoresis) and showed different results for the same bacterial populations, with some overlapping findings (Cho and Hwang, 2011; Fahlgren et al., 2010; Urbano et al., 2011). As these methods most likely reflect only the most abundant taxa due to the limited number of sequences obtained, 16S rRNA gene pyrosequencing has been successfully used to study bacterial populations in marine bioaerosol samples, enabling a better coverage of the

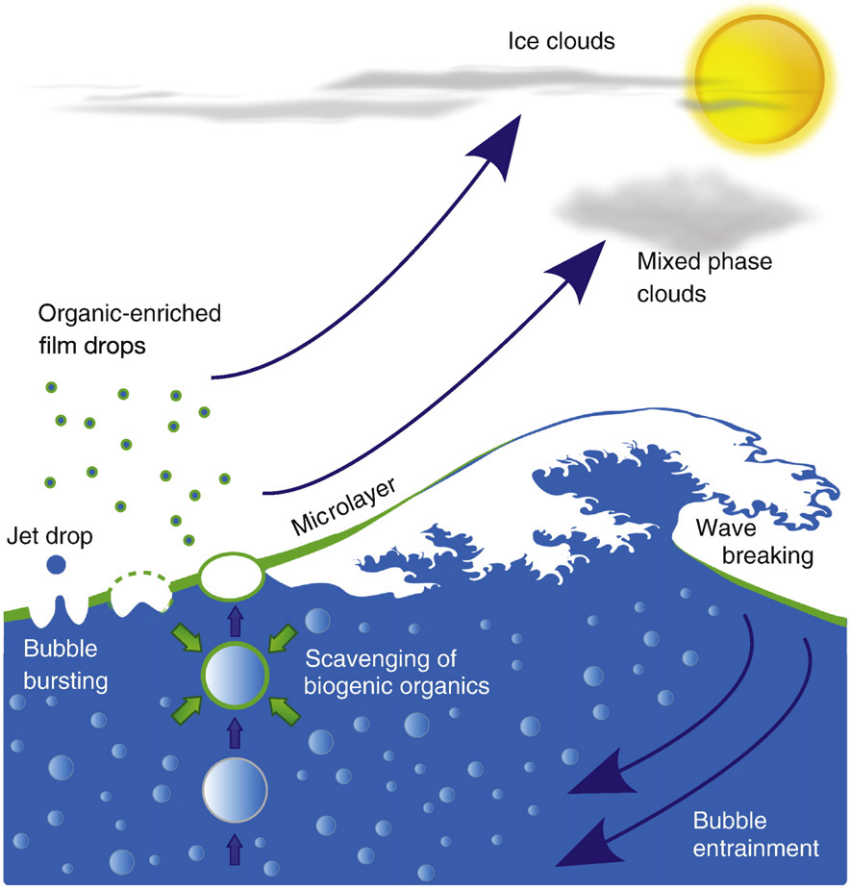

Fig. 16. Aerosol generation and enrichment of surface organic material (green layer) at the air-sea interface by bubble bursting. Reprinted with permission from Macmillan Publishers Ltd.: Nature. Wilson et al. (2015), copyright 2015.

whole marine bacterial community (DeLeon-Rodriguez et al., 2013; Seifried et al., 2015). Moreover, quantitative PCR has been applied to quantify selected health-relevant cyanobacteria and dinoflagellate species in marine air samples (Casabianca et al., 2013; Lang-Yona et al., 2014).

Other bioaerosol types like archaea, fungi, protozoa, and algae can also be ejected from the oceans into the atmosphere (Després et al., 2012; Elbert et al., 2007; Hamilton and Lenton, 1998; Mayol et al., 2014). Measurements on South Atlantic Ocean aerosol showed that biological particles account for 17% in number and 10% in volume concentration (Matthias-Maser et al., 1999). For the North Atlantic Ocean, the abundances of eukaryotic and prokaryotic microorganisms in the boundary layer ranged between 6×10^4 and 1.6×10^7 m^{-2} ocean surface, indicating a dynamic sea-air exchange with millions of microorganisms leaving and entering the ocean per square meter every day and 10% of microorganisms still airborne four days later (Mayol et al., 2014). In addition, other non-cellular particles, such as waste products or exudates of marine organisms, make up a large portion of microbially-derived matter in marine waters and affect the composition of marine atmospheric aerosol (Bigg and Leck, 2008; Burrows et al., 2013a, 2014; Wang et al., 2015). The global marine emissions of submicron primary organic aerosol particles by sea spray have been estimated to be 10 ± 5 Tg a^{-1} (Gantt and Meskhidze, 2013). Consequently, improving observations and understanding of the size-resolved organic fraction of sea spray emissions has been identified as high priority research topic (Meskhidze et al., 2013). These emissions can influence the number of cloud condensation nuclei available to marine clouds, which can affect their properties and brightness (Karydis et al., 2012; Moore et al., 2013). The resultant effects on clouds may be large enough to be observable by satellites, allowing top-down observational constraints on their magnitude. Recently, McCoy et al. (2015) analyzed seasonal and spatial patterns in the satellite-observed cloud droplet number concentration over the Southern Ocean (35–55°S latitude), where the ocean is the dominant source of particulate matter, and inferred an annual zonal mean radiative forcing of up to 1–2 W m^{-2} attributable to the influence of marine organic sea spray aerosol on cloud droplet number and, consequently, on cloud brightness.

Fungal spores and cell emissions from the oceans have been estimated to be around 10 Mg a^{-1}, six orders of magnitude smaller than land surface emissions (Elbert et al., 2007). Observed differences in fungal species richness in marine and continental air clearly demonstrate the presence of biogeographic patterns, and indicate that regional differences may be important for the effects of microorganisms on climate and public health (Fröhlich-Nowoisky et al., 2012). These findings also suggest that airflow patterns and the global atmospheric circulation are important for the evolution of microbial ecology and for the understanding of global changes in biodiversity. There is a need for more measurements of total concentration, fluxes, and ice-nucleating properties of all types of bioaerosols in the marine atmosphere to understand the importance of bioaerosols for the maintenance of biodiversity, climate, and health on a global scale (Burrows et al., 2009b; Mason et al., 2015; Pöschl, 2005). Moreover, deposited PBA particles in marine sediments, as well as in lake sediments and ice cores, can provide information about climatic changes of the past (Combourieu-Nebout et al., 2013; Kattel and Sirocko, 2011; Liu et al., 1998; Mueller et al., 2010; Schmiedl et al., 2010). For instance, pollen grains are well preserved in the sediment layers. They can be extracted from sediments and identified based on morphology, which allows a reconstruction of past vegetation patterns. Changes over time in the diversity and abundance of different types of pollen grains can indicate changes in vegetation that may be related to climate change or human influence. However, it is necessary to understand the source area of pollen, i.e., the influence of long-distance transported pollen, and the factors that influence the preservation, transport, and deposition of pollen grains in an aquatic environment in order to accurately interpret the pollen record (Barreto et al., 2012; Davis and Brubaker, 1973; Davis, 1968, 2000; Klemm et al., 2015; Matthias and Giesecke, 2014; Pittam et al., 2006). As reviewed by Davis (2000), different models have been developed to predict the size of the relevant source areas, how the ratio of regional to local pollen changes with lake size, or how landscape patterns will be reflected in pollen records. These models can help to choose lakes of appropriate size and to calculate the size of the expected source area. In addition, also biomarkers and DNA analysis can be used to investigate the relevance of different organisms in the past (Domaizon et al., 2013; Kyle et al., 2015; Okano et al., 2007; Romero-Sarmiento et al., 2011).

4.3. Pathogens and allergens

Bioaerosols can have infectious, allergenic, or toxic effects on living organisms, impacting health and agriculture on local, regional, and global scales. Many plant, animal, and human pathogens are dispersed through the air; some can travel over long distances spreading diseases across and even between continents (Brown and Hovmøller, 2002; Fisher et al., 2012). Several plant pathogens, including those causing rust, downy mildew, and powdery mildew diseases are responsible for significant economic losses in agriculture worldwide (Aylor and Taylor, 1982; Brown and Hovmøller, 2002; Burt, 1995; García-Blázquez et al., 2008; Lucas et al., 1992; Milgroom et al., 1996). For example, coffee leaf rust caused by the fungus *Hemileia vastatrix* is the most destructive disease of coffee in the world (Lucas et al., 1992). Urediniospores from infected and fallen coffee leaves are easily spread by wind or rain. Fig. 17 shows the symptoms of coffee leaf rust that include the appearance of orange-yellow powdery spots and early defoliation (Carvalho et al., 2011; Lucas et al., 1992).

Various major infectious diseases of humans and animals, like anthrax, foot-and-mouth disease, tuberculosis, Legionnaire's disease, influenza, and measles could be spread by airborne bacteria or viruses (Arzt et al., 2011; Langer et al., 2012; Riley, 1974; Shafazand et al., 1999). The inhalation of pathogenic viable airborne fungi, like *Aspergillus*, *Cryptococcus*, and *Pneumocystis* spp., into the lungs can cause invasive infections associated with mortality rates of up to 95% in infected populations, especially in individuals with impaired immune function (Brown et al., 2012; Lin et al., 2001; Yu et al., 2010). In particular, the spread of airborne pathogens within hospitals represents a permanent health challenge in infection control (Hoffman et al., 1999; Schaal, 1991). The transmission of pathogens and other bioaerosols between humans has long been a topic of research as humans harbor diverse microbes (including pathogens) in and on their bodies. Particularly in indoor environments, the presence and activities of humans can influence bioaerosol concentration. The emission of particles by breathing, sneezing, coughing, talking, and movement, as well as from resuspension of dust due to human activity, has been the focus of numerous indoor bioaerosol studies (e.g., Adams et al., 2015; Bhangar et al., 2014, 2015; Castillo et al., 2012; Hospodsky et al., 2012; Meadow et al., 2014, 2015; Morawska, 2006; Nazaroff, 2015; Noble, 1975; Qian et al., 2012, 2014; You, 2013). As discussed by Bhangar et al. (2015), many studies have not differentiated between direct emissions from the human body and resuspension of dust from surfaces during human activity, thus providing only overall emission rates. Chamber experiments offer a more controlled environment to study direct human emission rates under varying conditions (Adams et al., 2015; Bhangar et al., 2015; Hospodsky et al., 2012; Meadow et al., 2015; Nazaroff, 2015; You, 2013). Recently, Bhangar et al. (2015) found by measuring FBAP in a chamber study that approximately 10^6 human-associated particles are emitted into the surrounding air per human and hour under seated conditions (Bhangar et al., 2015). Other recent findings indicate that the microbial clouds released by humans are personalized and can be traced back to particular individuals (Meadow et al., 2015).

Different modeling strategies have been used to simulate the spread of human, animal, and plant pathogens, focusing on risk assessment and disease forecasting (Aylor, 2003; Davis, 1987; Isard et al., 2005; Van

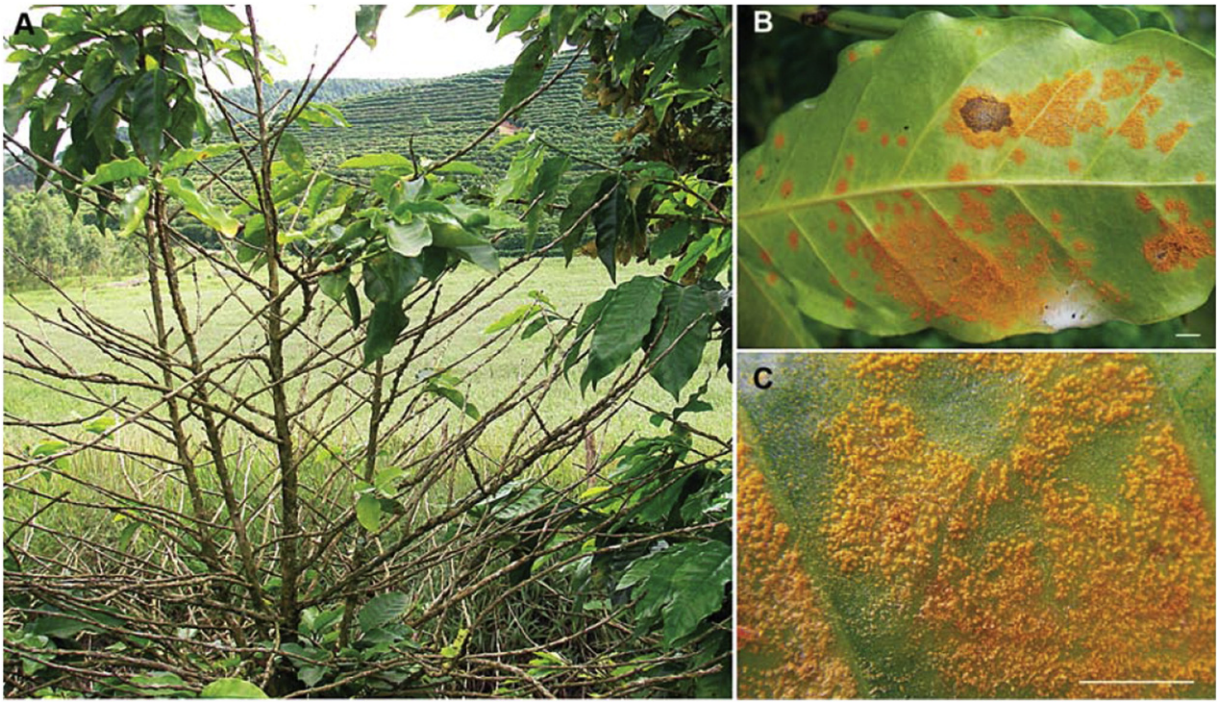

Fig. 17. Symptoms of coffee leaf rust *Hemileia vastatrix*: (A) defoliation, (B) leaf symptoms (bar = 0.5 cm), and (C) detail of suprastomatal uredinial pustules coalescing over lower leaf surface (bar = 0.5 cm).
Adapted from Carvalho et al. (2011).

Leuken et al., 2016; Yao et al., 1997). As suggested by Van Leuken et al. (2016), risk assessment models simulating the dispersal of pathogens need to be further improved by implementing well-quantified emission and inactivation rates as well as dose–response functions to better estimate infection probabilities.

Moreover, the inhalation and deposition of bioaerosols in various regions of the respiratory system can cause allergic or toxic responses in humans and animals. The deposition of inhaled particles in the respiratory tract depends on particle properties, airway morphology, and breathing characteristics (Hofmann, 2011; Hussain et al., 2011). Fig. 18 shows the size-dependent particle deposition in different regions of the respiratory tract. Particles larger than 0.5 μm are deposited by sedimentation and impaction mainly in the head airways. Particles smaller than 0.5 μm can reach the lower airways by diffusion. A more detailed description of particle deposition in the respiratory tract and lung deposition modeling can be found in related reviews and references therein (Hofmann, 2011; Hussain et al., 2011; Nazaroff, 2015).

Allergenic and toxic bioaerosols need not to be viable, as also dead cells or cell fragments may provoke the same adverse health effects. Examples for biological toxins found in air particulate matter are cell wall components of bacteria (endotoxins) or secondary metabolites produced by bacteria (exotoxins) or fungi (mycotoxins).

Exposure to mycotoxins after inhalation of mycotoxin-containing particles, such as fungal spores, is particularly relevant in farm environments or water-damaged buildings (Hintikka and Nikulin, 1998; Mayer et al., 2007; Nielsen, 2003; Robbins et al., 2000). Mycotoxins are a structurally diverse group of mostly low-molecular-weight compounds that have no apparent function in the fungal metabolism, but can have a variety of acute and chronic health effects in humans and animals, as recently reviewed by Ashiq et al. (2014); Edite Bezerra da Rocha et al. (2014), and Marroquín-Cardona et al. (2014).

Bacterial endotoxins are lipopolysaccharides (LPS), which are components of the outer cell membrane of gram-negative bacteria that can be released during cell lysis. They are of particular interest as they can induce strong inflammatory responses and symptoms like fever, headache, coughing, and respiratory distress (Degobbi et al., 2011; Douwes, 2003; Heederik and von Mutius, 2012; Longhin et al., 2013; Ortiz-Martínez et al., 2015; Rylander, 2002; Soukup and Becker, 2001; Vernooy et al., 2002). Elevated levels of endotoxins in air particulate matter were found in indoor air (Gehring et al., 2002; Gereda et al., 2000), in agriculture and related industries (Rylander, 2002; Spaan et al., 2006), as part of PM10 (Cheng et al., 2012; Heinrich et al., 2003; Morgenstern et al., 2005; Mueller-Annelling et al., 2004; Nilsson et al., 2011; Traversi et al., 2011; Wheeler et al., 2011), connected to microbial biomass (Woo et al., 2013), and to cyanobacteria and chlorophyll-a concentration (Lang-Yona et al., 2014).

In addition to LPS or endotoxin, bacteria can also produce toxic secondary metabolites. These exotoxins are secreted by some bacterial pathogens, such as some strains of *Corynebacterium diphtheria* (diphtheria toxin) (Hadfield et al., 2000) and *Bordetella pertussis* (pertussis toxin) (Mattoo and Cherry, 2005; Warfel et al., 2012), which can be transmitted through the air. Moreover, of particular concern are toxins produced by cyanobacteria. Cyanobacteria are widespread and abundant organisms in terrestrial, as well as aquatic environments, which produce neurotoxins, cytotoxins, dermatotoxins, and different types of hepatotoxins (Codd et al., 1997, 1999; Cox et al., 2005; Kaasalainen et al., 2012; Oberholster et al., 2004; Wiegand and Pflugmacher, 2005). Whereas neurotoxins inhibit neurotransmission by a variety of mechanisms, frequently causing death of the exposed organisms, hepatotoxins, comprising the cyclic peptide groups of microcystins and nodularins as well as the cyclic guanidine alkaloid cylindrospermin, are hepatotoxic, causing severe and sometimes toxic health effects in domestic and wild animals as well as in humans (Codd et al., 1997, 1999). Both neurotoxins and hepatotoxins are produced by some aquatic genera, as e.g. *Anabaena*, *Oscillatoria*, *Microcystis*, and *Aphanizomenon*, and hepatotoxins are also produced by a variety of terrestrial lichens with cyanobacterial photobionts (Kaasalainen et al., 2012). Exposure to cyanotoxins has been described to occur via skin contact, inhalation, ingestion, and haemodialysis (Backer et al., 2010; Benson et al., 2005; Codd et al., 1999; Wood and Dietrich, 2011).

One neurotoxin produced by cyanobacteria, β-methylamino-L-alanine (BMAA), is suspected to contribute to human neurodegenerative

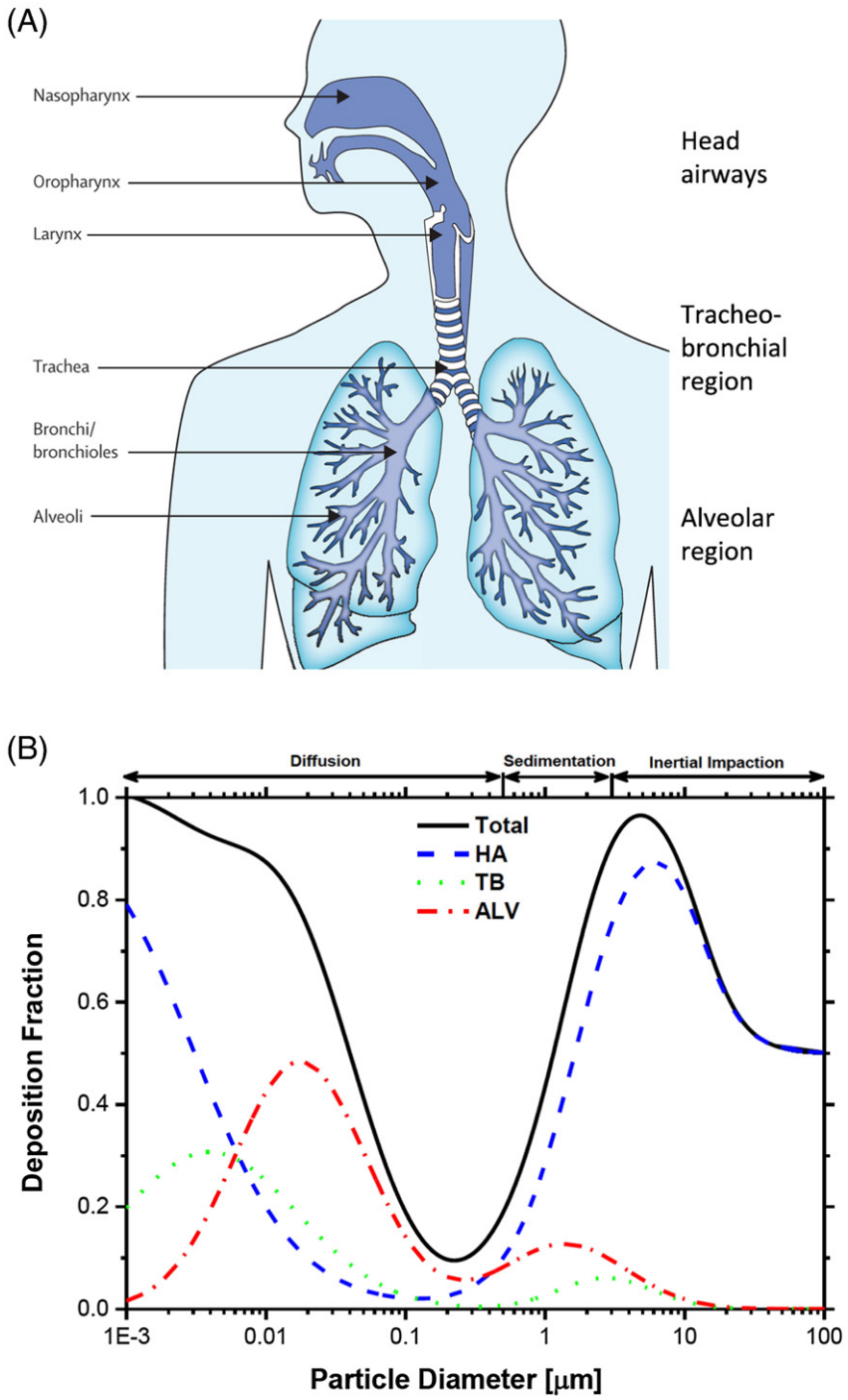

Fig. 18. Deposition of inhaled particles: (A) human respiratory tract and (B) predicted total and regional particle deposition in relation to particle size, based on the International Commission on Radiological Protection (ICRP) deposition model for nasal breathing and light exercise and deposition mechanisms. HA: head airways; TB: tracheobronchial region; ALV: alveolar region.
(A) Reprinted from The Lancet 383, Guarnieri and Balmes (2014), copyright 2014, with permission from Elsevier.

diseases, as the same substance has been identified in the brain and cerebrospinal fluid of amyotrophic lateral sclerosis (ALS) and Alzheimer's disease victims (Cervantes Cianca et al., 2012; Field et al., 2013; Metcalf and Codd, 2009) and has been shown to cause neuronal changes in animal experiments (Karlsson et al., 2012; Okle et al., 2013; Zhou et al., 2010). The neurotoxin BMAA is produced by free-living and symbiotic cyanobacteria, diatoms, and dinoflagellates in marine, freshwater, and terrestrial environments (Cervantes Cianca et al., 2012; Cox et al., 2005; Jiang and Ilag, 2014; Jiang et al., 2014a, 2014b; Lage et al., 2014). Uptake of BMAA has been suggested to happen via consumption of contaminated food and exposure to water harboring cyanobacterial blooms, as well as via aerosolization, which may happen in cooling towers (Stommel et al., 2013).

Important sources of aeroallergens are wind-dispersed pollen from trees, grasses, and weeds, fungal spores and hyphae, animal dander, and house-dust mite excretions (Buters et al., 2015; D'Amato et al., 2007; Esch et al., 2001; Green et al., 2003, 2005,2006, 2011; Grinn-Gofroń and Rapiejko, 2009; Horner et al., 1995; Jochner et al., 2015; Shiraiwa et al., 2012a; Twaroch et al., 2015; Vara et al., 2016). Allergies and associated respiratory diseases represent a

serious health challenge of increasing importance in many countries (D'Amato et al., 2007; Ring et al., 2001). Pollen allergies affect up to 40% of the population in industrialized countries and have become a global problem (D'Amato et al., 2007; Shiraiwa et al., 2012a). Furthermore, up to 30% of atopic individuals are sensitized to one or more fungal allergens (Esch et al., 2001).

A common type of allergy is mediated by the production of specific IgE antibodies against otherwise harmless proteins, then called allergens (Traidl-Hoffmann et al., 2009). Proteins account for up to 5% of urban air particulate matter, and interactions of these proteins with ozone, nitrogen dioxide, sulfur dioxide, and air particulate matter can lead to modified proteins with modified allergenic potential (Franze et al., 2005; Gruijthuijsen et al., 2006; Knox et al., 1997; Lang-Yona et al., 2016; Shiraiwa et al., 2012a). Many studies have demonstrated an increase in sensitization and allergic symptoms and correlations with high levels of anthropogenic air pollution, but the underlying mechanisms remain unclear (D'Amato, 2000; D'Amato et al., 2001, 2007, 2013; Gehring et al., 2010; Morgenstern et al., 2008).

The prevalence and severity of allergic diseases and asthma are likely to increase further through anthropogenic air pollution and climate change related factors. Effects of climate change on the physiology and distribution of plants and fungi have been shown in several studies (Cecchi et al., 2010; Reid and Gamble, 2009). For instance, increasing temperature and CO_2 concentration can affect fungal fruiting patterns and sporulation (Gange et al., 2007; Klironomos et al., 1997; Wolf et al., 2010), pollen production and pollination periods in plants (Zhang et al., 2014a, 2014b; Ziska and Caufield, 2000), the allergen content of spores and pollen (Lang-Yona et al., 2013; Singer et al., 2005), and the distribution patterns of aeroallergens (Cecchi et al., 2010; Reid and Gamble, 2009).

Moreover, both changes in climate and an intensification of land use have been shown to cause an increase in dust storm frequency and intensity (McLeman et al., 2014; Stanelle et al., 2014; Stocker et al., 2013), and dust particles are known to carry biological and organic components with pathogenic and allergenic properties (Chen et al., 2010; Esmaeil et al., 2014; Goudie, 2014; Griffin, 2007; Hallar et al., 2011; Kellogg and Griffin, 2006; Leski et al., 2011; Ortiz-Martínez et al., 2015; Schlesinger et al., 2006) but possible synergistic effects of different dust constituents on human health, the propagation of pathogenicity along the dust event, and sources of health relevant PBA are still not well characterized.

Anthropogenic air pollution, thunderstorms, and humidity have been shown to influence allergen release from pollen and spores (Behrendt and Becker, 2001; Behrendt et al., 1997; Buters et al., 2015; Cecchi et al., 2010; Grote et al., 2001; Motta et al., 2006; Ouyang et al., 2016; Schäppi et al., 1997). During a thunderstorm, pollen and spores may break by osmotic shock and release allergens into the atmosphere leading to asthma outbreaks known as thunderstorm asthma (Behrendt and Becker, 2001; Cecchi et al., 2010; Laskin et al., 2016; Taylor and Jonsson, 2004; Taylor et al., 2002). Thunderstorms also favor an increase of fungal spore counts, further contributing to asthma epidemics (Behrendt and Becker, 2001; Cecchi et al., 2010; D'Amato et al., 2007). Furthermore, under humid conditions pollen grains release proinflammatory substances (Bacsi et al., 2006; Behrendt and Becker, 2001; Miguel et al., 2006). The release of these substances was found to be higher for pollen collected near roads with heavy traffic (Behrendt and Becker, 2001). Free allergens and related compounds can bind to fine particulate matter, such as diesel exhaust particles, leading to the generation of allergen-containing aerosols in the submicrometer range that can be transported deep into the airways (Knox et al., 1997; Namork et al., 2006; Ormstad, 2000). Additionally, traffic-related pollutants can also modify the immune system response to the allergen itself. Diesel exhaust particles can modify allergen presentation, whereas gaseous pollutants like O_3, SO_2, and NO_2 can enhance immune system response by enhanced antibody production and late inflammation (Saxon and Diaz-Sanchez, 2005). The impact of air pollutants and environmental factors on PBA allergenicity still needs to be better characterized. Especially, further investigation is required in order to better understand the complex interactions of modified allergens within the human body.

5. Future perspectives

Fig. 19 shows an overview of important and promising areas of future research, which can be coarsely divided into the three main fields: (1) bioparticle identification and characterization; (2) atmospheric transport and transformation; and (3) ecosystem interactions of bioaerosols. Studies within these fields could help to close or narrow the large gaps of knowledge outlined in this review and to constrain uncertain parameters and assumptions, which will allow to improve modeling of the effects of bioaerosols on climate, health, and ecosystems on local, regional, and global scales.

(1) For comprehensive taxonomic and chemical identification, characterization, and quantification of bioaerosol particles, their viability and metabolic state, the wide range of advanced and innovative online and offline measurement methods outlined in Sect. 2 should be applied and further developed (NGS sequencing, fluorescence detection, etc.). An important aspect is the coupling of detailed biological analyses and information with the real-time data of modern physical and chemical techniques, including genomic, proteomic, and metabolomic approaches. The development and application of standardized sampling and analysis techniques appears necessary to achieve consistency between different measurements and datasets.

(2) To understand the spatial and temporal dynamics of atmospheric bioaerosols, the pathways of emission, transport, and transformation in the atmosphere need to be analyzed from molecular to global scales. Major challenges include the quantitative characterization of exchange between surface, planetary boundary layer, and free troposphere. For this purpose, ground based measurements have to be combined with tall tower and aircraft measurements as well with satellite remote sensing to obtain information on the vertical and horizontal distribution of bioparticles. Particularly interesting are the distribution patterns of IN-active microorganisms and detached nanometer-sized IN-active particle fragments and macromolecules (also called “nano-INP” or “INM”), and their interactions with clouds and precipitation. These have to be elucidated on microscopic as well as regional and global scales to validate or discard the bioprecipitation feedback hypothesis and its relevance for the Earth system (Sect. 3.3). Other important aspects are the effects of physical, chemical, and biological transformation, aging, and stress upon exposure to atmospheric oxidants, radiation, and changes of temperature, pressure, and humidity (osmotic shock) on the emission, vitality, and viability of airborne bioparticles. These effects need to be quantified in chamber and field studies under relevant conditions to fully understand the impact of atmospheric transport on the adaptation and resilience of aerially disseminated organisms (wind-pollinated plants, sporulating microbes) and their influence on the functioning of ecosystems.

(3) Representative measurements and climatologies of bioaerosols in and above ecosystems along the climatic gradients from tropical to polar and continental to marine regions are required to unravel the interdependence of biodiversity and biogeography in the air and at the Earth surface, as well as the impact of environmental conditions, climate, and land use change on bioaerosol emission and deposition, related biogeochemical cycles, and public health. Key aspects are the roles of cryptogamic covers on ground and plant surfaces, nitrogen cycling microbes, and bioprecipitation feedbacks in the co-

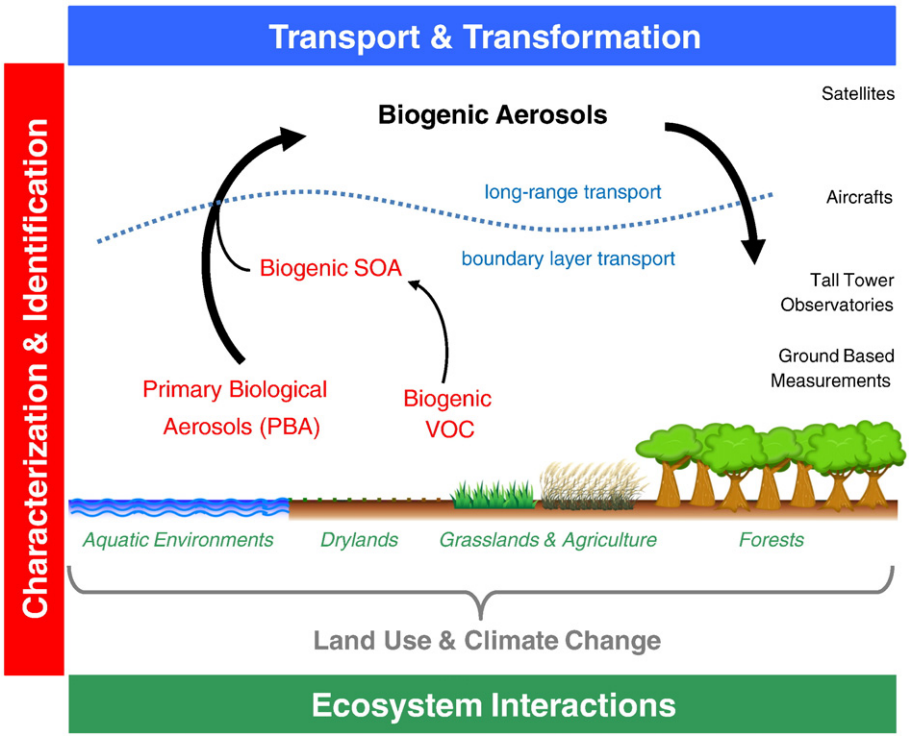

Fig. 19. Key aspects and areas of research required to determine and quantify the interactions and effects of biogenic aerosol particles in the Earth system, including primary biological aerosols (PBA) directly emitted to the atmosphere and secondary organic aerosols (SOA) formed upon oxidation and gas-to-particle conversion of volatile organic compounds (VOC).

evolution of life and climate, as well as the spread and effects of pathogens and allergens interacting with air pollutants. To address these issues, the results of comprehensive observations and bioaerosol monitoring in today's atmosphere (e.g., by NGS sequencing, fluorescence detection, and chemical analysis) should be compared and combined with climate archive analyses (e.g., pollen, spores, biomarkers, and DNA in lake and ocean sediments) and implemented in ecosystem and Earth system models. Ecosystem and Earth system model descriptions and parameterizations of all bioaerosol properties and processes outlined above are relevant for our understanding of the origins and spread of life on Earth and for the modeling of ecosystem interactions in Earth's history and future climate.

To tackle the wide range of open questions outlined above, it will be necessary to further intensify collaboration and interdisciplinary exchange across the fields of chemistry, Earth, and life science, in particular between the scientific communities of atmospheric chemistry and physics, climate and aerosol science, biogeochemistry and ecology, air quality and public health, forestry and agriculture, and geo- and bioinformatics.

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