MINIREVIEW

Microorganisms in the atmosphere over Antarctica

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Abstract

Antarctic microbial biodiversity is the result of a balance between evolution, extinction and colonization, and so it is not possible to gain a full understanding of the microbial biodiversity of a location, its biogeography, stability or evolutionary relationships without some understanding of the input of new biodiversity from the aerial environment. In addition, it is important to know whether the microorganisms already present are transient or resident – this is particularly true for the Antarctic environment, as selective pressures for survival in the air are similar to those that make microorganisms suitable for Antarctic colonization. The source of potential airborne colonists is widespread, as they may originate from plant surfaces, animals, water surfaces or soils and even from bacteria replicating within the clouds. On a global scale, transport of air masses from the well-mixed boundary layer to high-altitude sites has frequently been observed, particularly in the warm season, and these air masses contain microorganisms. Indeed, it has become evident that much of the microbial life within remote environments is transported by air currents. In this review, we examine the behaviour of microorganisms in the Antarctic aerial environment and the extent to which these microorganisms might influence Antarctic microbial biodiversity.

The atmosphere

Structure and composition

The atmosphere can be divided into a number of vertical segments (Fig. 1a and b). The lowest layer (or troposphere) begins at the Earth's surface and extends to about 10 km, although its lower boundary tends to be higher nearer the equator and lower nearer the poles (Kley, 1997). This is also the region of weather (Fig. 2), with vertical movements of air pockets. The troposphere has a distinctly nonuniform, layered structure. The next layer is the stratosphere, which extends up to about 50 km, and where the airflow is mostly horizontal. The stratosphere contains the ozone layer, an important UV light filter. The mesosphere (*c.* 50–80 km) lies above the stratosphere, and is the region in which air masses are relatively well mixed together, and where temperatures can drop to $-100\,^{\circ}C$ (colder than Antarctica's lowest recorded temperature). The thermosphere (to >600 km), where temperatures increase to 1000–1500 °C, lies above this layer, then the ionosphere, the part of the atmosphere ionized by solar radiation, and finally the exosphere (up to 10 000 km), which merges with space.

The troposphere contains roughly 80% of the total mass of gas in the atmosphere and 50% of this mass is located below 5 km. This layer, therefore, contains much of the microbial life associated with the atmosphere (Fig. 1c). Microorganisms have also been isolated from the stratosphere, and these have been considered in a number of existing reviews (e.g. Imshenetskii *et al.*, 1986). Stratospheric isolates include two bacteria (*Bacillus simplex* and *Staphylococcus pasteuri*) isolated from an altitude of 41 km and a single fungus, *Engyodontium album* (Limber) de Hoog (Wainwright *et al.*, 2003). Bacteria have even been found 70 km above the Earth's surface using high-altitude rockets (Imshenetskii *et al.*, 1978). Partitioning of such microorganisms between different vertical segments could result from thermal boundaries and the thin buffer zones (or pauses), for example the tropopause, the boundary between the troposphere and the stratosphere.

FEMS MICROBIOLOGY ECOLOGY

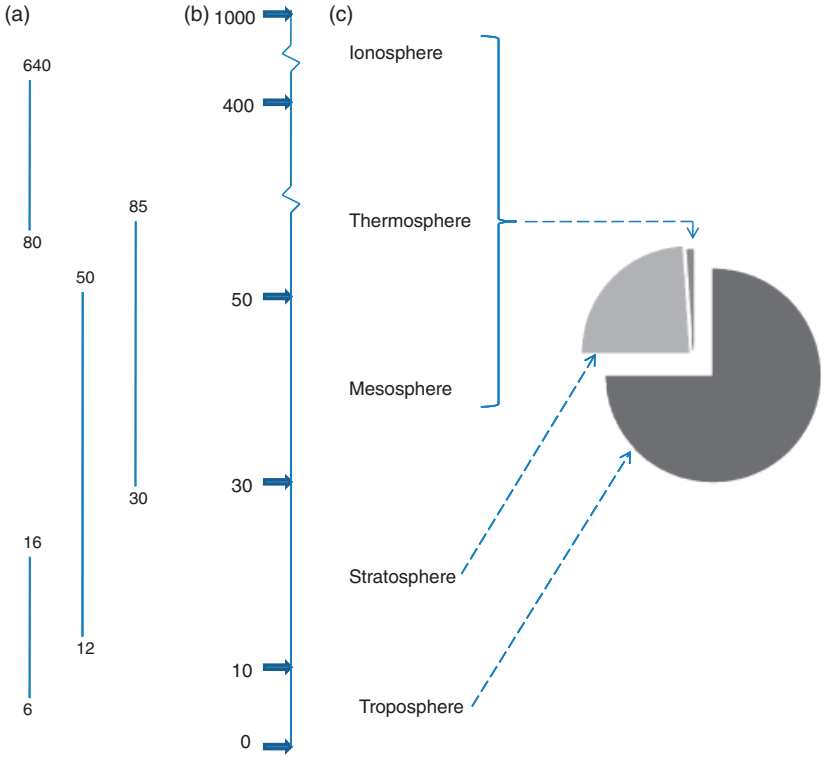

Fig. 1. Schematic diagram of layers within the atmosphere showing (a) ranges given in different sources (boundaries are not fixed and vary with latitude), (b) the heights of different layers in kilometres and (c) the proportion of aerial microorganisms found in each of the atmospheric layers.

Fig. 2. The Antarctic troposphere. Photograph courtesy of Peter Bucktrout (BAS).

The Antarctic atmosphere

Antarctica is the most remote continent on Earth. It is particularly well suited for studies involving the aerial transport and survival of microorganisms, as it is isolated from the rest of the world by the Southern Ocean and Antarctic circumpolar current. Where this meets the other world oceans (the Antarctic convergence), the differential temperature of the air masses above warmer low-latitude water and colder high-latitude water discourages mixing. At its narrowest, the Southern Ocean is 1000 km wide between South America and the northern tip of the Antarctic Peninsula. Therefore, this ocean is a major barrier to potential colonizers of Antarctica. In Antarctica itself, the greatest terrestrial biodiversity is in the maritime regions, where numerous moss and lichen species are found together with Antarctica's only two flowering plant species (*Deschampsia antarctica* and *Colobanthus quitensis*) (Smith, 1994). The biodiversity of larger organisms generally declines with increasing latitude as conditions get colder and drier and the length of the growing season decreases (Convey, 2001). Indeed, continental Antarctica is occupied by only the most durable species, such as lichens and the microorganisms. This clear latitudinal trend observed for the macrobiota does not necessarily apply to the microbiota. On the basis of culture-dependent studies, it was concluded that bacteria from Antarctic soils are probably cosmopolitan, similar to those found in soils elsewhere in the world; however, more recent molecular (DNA)-based investigations indicate that there are novel species and genera in Antarctica (Adams *et al.*, 2006; Aislabie *et al.*, 2006). The total number of bacteria in Antarctic soils depends strongly on the thermal regimen and the availability of water, but even in Dry Valley soils, numbers may be underestimated if appropriate enumeration techniques (which perform optimally under dry, low organic matter conditions) are not used (Cowan *et al.*, 2002). Within frost-sorted polygon soils, the patterns of eukaryotic microbial diversity are inconsistent with those of higher groups. Lawley *et al.* (2004) found only limited support for a systematic decrease in diversity

with latitude, and then only at the level of a gross comparison between maritime (Antarctic Peninsula/Scotia Arc) and continental Antarctic sites. While the most southerly continental Antarctic site studied was found to be three to four times less diverse than all maritime sites, there was no evidence of a trend of decreasing diversity across the entire range of the maritime Antarctic (60–72°S). Their observations might also provide some support for the global ubiquity hypothesis put forward by Finlay (2002); however, the very limited overlap found between the eukaryotic biota of the different study sites, combined with their generally low relatedness to existing sequence databases, indicated a high level of Antarctic site isolation and possibly endemicity, a pattern not consistent with similar studies on other continents.

Airborne microbial biodiversity

Microorganisms present in the atmosphere over Antarctica

Biological material present in Antarctic air at lower levels may include moss spores, pollen (e.g. from *D. antarctica*), fungal spores, bacteria (including cyanobacteria), algal propagules, viruses, lichen propagules, tardigrade cysts, nematodes and arthropod fragments (Burckle *et al.*, 1988; Wynn-Williams, 1991; Marshall, 1996a, b, 1997). However, only a few studies have been conducted to date on the ecology or function of microorganisms in the aerial environment, and yet aerial microbiota may have an important role in the functioning of the environment, particularly as cloud condensation nuclei and through the alteration of atmospheric chemistry (Bauer *et al.*, 2002, 2003; Leck & Bigg, 2005).

Early attempts to study the aerobiology of biological material in Antarctica (and indeed, the rest of the globe) were severely restricted by the techniques available at the time for particle detection and identification (Cameron *et al.*, 1972). Microscopy, for example, only allows identification of particles with characteristic morphologies, and these represent only a small proportion of the airborne material. Damage to these characteristic particles in the air column by high UV-B, low temperatures and extreme desiccation may exacerbate the situation by making them impossible to identify. Culture techniques on solid or liquid media may confirm if air-transported propagules are viable, but this technique is inappropriate for estimating total biodiversity due to loss of viability through particle damage in transit, or inappropriate culture conditions for specific microbial groups. As a result, estimates of biodiversity entering Antarctica from the surrounding continents based on these techniques are likely to be underestimated or skewed.

Aerial microbiota are diverse and differ greatly in their taxonomy, physical, ecological, behavioural and pathogenic characteristics. Some patterns may, however, be discerned. It has been observed, for example, that Gram-positive rods are often more prevalent than Gram-negative rods, although this might be due to the presence of spores. The culturability of collected airborne microbiota also varies widely and is affected by several variables such as temperature, time, nutrients and species. In a study of airborne actinomycetes, Reponen *et al.* (1998) found that the relative recovery of the spores on agar media ranged from 0.5% to 35%. Commonly encountered bacterial genera found in both air samples and the Antarctic include – *Staphylococcus*, *Bacillus*, *Corynebacterium*, *Micrococcus*, *Streptococcus*, *Neisseria* and *Pseudomonas*. Commonly encountered fungal genera include – *Penicillium*, *Aspergillus*, *Cladosporium*, *Alternaria*, *Aureobasidium*, *Botryotrichum*, *Botrytis*, *Geotrichum*, *Staphylotrichum*, *Paecilomyces* and *Rhizopus*.

Abundance and variation

Very few studies have been conducted on Antarctic air samples to date; so much of what we know about the probable behaviour of airborne microbiotia comes from studies undertaken in other parts of the world. For example, tropospheric microbial populations isolated from clouds over France contained up to 8×10^4 bacteria mL^{-1} of cloud water and were capable of growing at low temperatures; many were pigmented or were spore-formers of genera commonly found in terrestrial soil and water (Amato *et al.*, 2007a).

Variation in the abundance of airborne microorganisms is extremely high; for example, Lighthart & Shaffer (1995) found concentrations of airborne bacteria with a maximum of 1368.5 CFU m^{-3}, with a coefficient of variation of 90.5% and a mean of 121.3 CFU m^{-3} above a temperate field. This variation can operate over a number of different time scales, which include instantaneous effects of local microclimatic conditions, diurnal periodicity (Hasnain *et al.*, 2005; Rossi *et al.*, 2005) and seasonality for both bacteria (Marafie & Ashkanani, 1991; Choi *et al.*, 1997; Mahdy & El Sehrawi, 1997; Kruczalak *et al.*, 2002; Oppliger *et al.*, 2005) and fungi (Shelton *et al.*, 2002), with peak abundances tending to occur over the summer, but also to some extent in spring and autumn. A number of factors are thought to influence this periodicity, particularly meteorological conditions (Lighthart & Shaffer, 1995), including mean, minimum and maximum, temperature, dew point temperature, air pressure (Stennett & Beggs, 2004), the solar radiation cycle (including both diurnal and annual cycles), topography, ground heating by the sun or sea breezes, source strength and human activities (Lighthart, 1999). Indeed, spring airborne bacterial populations may be more sensitive to, and/

or extensively exposed to, environmental stresses (starvation, sunlight, etc.) and aerosolization, and thus fewer culturable bacteria per particle might be expected (Tong & Lighthart, 2000).

Aerial growth and survival

The question of whether airborne cells are actively growing in aerosols was answered first by Dimmick *et al.* (1979), who demonstrated that bacteria could divide on airborne particles, increasing from 7.3×10^5 to 1.4×10^6 cells L^{-1} within 6 h. However, considering the fact that different cloud types can persist for several days or weeks in the atmosphere before dissolving and being precipitated, respectively, it would be more accurate to see microorganisms as transients. Here, the huge challenge would be to survive and reproduce if the niche to which they are already adapted is present at the site of deposition, readapt to the new ecological niche upon deposition or remain dormant pending some future change in the environment. However, there are few reliable figures for how long, or how effectively, viability is maintained during aerial dispersal. Variability of residence time in the atmosphere can depend on temperature, wind, relative humidity (RH), convection and turbulences in both long- and short-term cycles. All these factors have an impact on the survival of microorganisms that can often travel as hitchhikers on particles such as mineral particles, dust, pollen, spores, organic debris or even hailstones (Mandrioli *et al.*, 1973). After their transitory passage through the atmosphere and subsequent deposition, bacteria may influence the composition of microbial assemblages in snow, soils, lake water and oceans, and the metabolic pathways and food webs in those environments, depending on their abundance and survival rates. Their ultimate trajectory can then have ecological consequences on the habitats in which they are deposited, especially if these habitats are remote and pristine like polar ice caps or high-altitude areas.

The limiting factors for microbial growth in this seemingly hostile environment are manifold (Fig. 3). For example, low pH could severely impede bacterial metabolism, but thanks to the buffering of ammonia and alkaline dusts, these values are kept between pH 5.4 and 6.8, and dissolved organic carbon concentrations can reach several mg L^{-1}, typical for lake water conditions. Natural solar radiation at high altitudes may strongly inhibit microbial activity, but clouds themselves can provide shading from damaging and bactericidal UV radiation.

Adaptation

There are a number of ways in which different microorganisms are adapted to aerial transport and survival, through tolerance of cold, low available water and UV radiation, using spores, mini cells and other small resistant cell forms. One particular adaptation is the ability to withstand long-term natural cryopreservation – samples of permafrost sediments with ages from 5–10 thousand to 2–3 million years have been found to contain viable micromycete and bacterial cells (Kochkina *et al.*, 2001). Another potential response might be to remain viable but not divide in transit. Hamilton & Lenton (1998) proposed that microorganisms of the atmosphere could use chemical induction of water condensation to enable or increase their wind dispersal between their aquatic, terrestrial or epiphytic growth sites.

Fig. 3. Extreme selection pressure; the low air temperatures experienced during the Antarctic winter at Signy Island are sufficiently low to instantly freeze boiling water. Photograph courtesy of David Barnes (BAS).

Airborne microbial activity

Cloud condensation nuclei, ice nuclei and cloud coverage

Bacteria can play an active role in ice nucleation and in creating precipitation in some types of clouds (Morris *et al.*, 2008). Supercooled water needs a surface on which to freeze

and this could be provided by mineral particles, bioaerosols or microbial cells. Schnell (1976) stated that bacteria attached to mineral particles were responsible for ice nucleation rather than the mineral particles themselves. Nowadays, the microbial ability to act as an ice nucleus is crucial for agriculture where ice nucleation can cause frost injuries to plants even at relatively warm temperatures close to the freezing point of water (Morris *et al.*, 2004). The most prominent bacterium with the ice nucleation gene is *Pseudomonas* spp., although ice nucleation-negative species have been detected in cloud samples collected from the Northern Hebrides (Ahern *et al.*, 2006). The protein is located in the surface of the outer membrane and serves as a template for the alignment of water molecules for ice crystallization. Less ice nucleating activity would certainly increase the lifespan of clouds and would therefore favour bacterial dispersal and ubiquity; however, more activity may, in itself, lead to faster release from the clouds and potentially greater environmental exposure. Depending on the abundance of bacteria in the atmosphere, cloud condensation capability is implicated in the alteration of cloud coverage (Ariya & Amyot, 2004).

Role of airborne microorganisms in atmospheric chemistry

With the early recognition that the atmosphere is carrying organic particles, it can be stated with confidence that the presence of microorganisms can influence atmospheric chemistry. Atmospheric aerosol samples can contain about 20% carbonaceous material in relation to the total aerosol mass (Bauer *et al.*, 2002). This organic input is a dynamic process (Sattler *et al.*, 2001), which suggests that the atmosphere is not only a conveyor of organic matter but also a habitat where significant bacterial processes take place during transport. Tropospheric bacterial populations isolated from clouds are capable of metabolizing the major organic acids present in cloud water *in situ*, such as formate, acetate and lactate, and so could play a role in cloud chemistry (P. Amato, pers. commun.). How strongly bacterial processes influence transformations of organic and inorganic components of the atmosphere is still to be studied, but they cannot be neglected: bacteria grow and divide, consume oxygen and produce proteins and a plethora of metabolites within the atmosphere at or below 0 °C (Sattler *et al.*, 2001). The ability to alter organic compounds in cloud droplets is connected to the availability of nutrients, temperature and liquid water, which is mainly available as supercooled water. According to Rosenfeld & Woodley (2000), supercooled water can be found at surprisingly low temperatures such as −37.5 °C.

Airborne microorganisms were originally termed 'spora', assuming they were inert or inactive. Consequently, the atmospheric environment was considered primarily as a mere conveyor, although polluted fog-water rich in nutrients, for instance, may provide a good substratum for microorganisms (Fuzzi *et al.*, 1997; Table 1). The clean and cold atmosphere of high altitudes, however, was not regarded as a suitable place for bacterial growth, until it was recognized that bacteria could also grow and metabolize in supercooled cloud droplets (Sattler *et al.*, 2001). Although temperatures in the atmosphere are mainly $< 0\,^{\circ}C$, the nutrient conditions of cloud and rainwater can be more favourable than in many oligotrophic freshwater lakes with average levels for sulphate (May: $96\,\mu eq\,L^{-1}$, November: $64\,\mu eq\,L^{-1}$) and nitrate (May: $27\,\mu eq\,L^{-1}$, November: $32\,\mu eq\,L^{-1}$) determined for alpine systems (Brantner *et al.*, 1994). Cloud water often contains rather high amounts of organic acids and it has been shown by Herlihy *et al.* (1987) that bacteria are able to utilize these organic compounds, albeit at room temperature. In addition, several alcohols, such as dodecanol, tetradecanol, hexadecanol and octadecanol, are constituents of the organic portion of the atmosphere in concentrations up to $1\,\mu g\,L^{-1}$ (Limbeck & Puxbaum, 2000). It is not clear, however, whether alcohols in cloud water and precipitation are produced or used by microorganisms, although it is known that the concentration of alcohols largely exceed that which might be expected to be produced by the bacterial biomass present in the cloud, suggesting an alternative source. Once precipitated, the microbial community is therefore also capable of interacting in the snow pack at the interface of snow and air where the bacterial origin is most likely to be the air.

Aerial dispersal and colonization

Movement of particles in the atmosphere

Hundreds of millions of tonnes of dust (along with viable microorganisms, macro- and micronutrients, trace metals and a variety of organic contaminants) are transported annually between continents. The majority of microorganisms in aerosols are found to be embedded in organic particles, and large portions of microorganisms in the sea-surface microlayer are associated with particles – while in subsurface waters most of them are free living (Aller *et al.*, 2005).

The dispersion of bacteria, algae, fungi and even larger organisms mainly by the wind has been known for decades. However, the introduction of nonindigenous species into new regions is rarely a result of aerial transfer alone, and the inherent ability to be transported in the atmosphere can determine the invasive potential of microorganisms once introduced (Isard *et al.*, 2005). For example, it has been suggested that *Phragmidium violaceum* was introduced to New Zealand by air currents, and that the inocula

Table 1. Antarctic atmosphere chemistry

Inorganics		
Coastal regions	ng m^{-3}	Wolff *et al.* (1998)
Sea salt	200–1400 (annual mean)	Wagenbach *et al.* (1998a)
Methanesulfonate	15 (annual mean)	Minikin *et al.* (1998)
Sulphate	151 (annual mean)	Minikin *et al.* (1998)
Nitrate	20–70 (range)	Wagenbach *et al.* (1998b)
Ammonium	~12.5 to 140–230 (range)	Legrand *et al.* (1998)
Black carbon	0.3–2 (monthly mean)	Wolff & Cachier (1998)
Central Antarctica	ng m^{-3} (range)	Jones *et al.* (2008)
Sea salt	0–45	Jourdain *et al.* (2008)
Central Antarctica	ng m^{-3} (mean)	Weller & Wagenbach (2007)
Methanesulphonate	17/44	Kohnen/Neuymayer stations
Sulphate	90/150	
Chloride	38/480	
Nitrate	25/42	
Sodium	24/270	
Ammonium	(48)/6.2	
Organics	pptV (annual mean)	
Ethane	186	Read *et al.* (2007)
Propane	31	Read *et al.* (2007)
Iso-butane	3.2	Read *et al.* (2007)
n-Butane	4.9	Read *et al.* (2007)
Acetylene	19	Read *et al.* (2007)
Acetic acid	52 (July) to 698 (January)	Legrand *et al.* (2004)
Formic acid	60 (June) to 311 (November)	Legrand *et al.* (2004)
Dodecanol	$< 1\ \mu g\ L^{-1}$	Limbeck & Puxbaum (2000)
Tetradecanol	$< 1\ \mu g\ L^{-1}$	Limbeck & Puxbaum (2000)
Hexadecanol	$< 1\ \mu g\ L^{-1}$	Limbeck & Puxbaum (2000)
Octadecanol	$< 1\ \mu g\ L^{-1}$	Limbeck & Puxbaum (2000)

could have taken 6 years to cross the Tasman Sea (McKenzie, 1998).

Aerosolization is potentially an important long-distance dispersal mechanism and may account for observed cosmopolitan distributions of some bacteria. Marine aerosols are formed primarily by the eruption of rising bubbles through the sea-surface microlayer and aerosol formation is the main vector for transport of bacteria and viruses across the air–sea interface (Aller *et al.*, 2005). Interhemispheric transport of viable fungi and bacteria with soil dust has been demonstrated in the tropics (Prospero *et al.*, 2005), and has also been shown to follow a clear meteorological and seasonal pattern. The strong association of cultivable organisms with dust would suggest that environmental factors such as UV irradiance might be relevant to viability in the aerial environment.

Depending on the type of cloud, air and water masses move vertically or horizontally. Therefore, for instance, clouds of the cumulonimbus type might be important for the 'pick-up' of lofted cells but are not relevant for any horizontal and long-term transport. Cirrus clouds, which appear in higher altitudes and therefore can cover longer distances, can carry bioaerosols over oceans, which are an important source of microorganisms found in clouds (Amato *et al.*, 2007b).

Dispersal

The airborne route is probably the most important dispersal mechanism for fungi. Indeed, the long-distance transport of plant pathogenic fungi takes place primarily in the planetary boundary layer of the atmosphere, which extends from about 50 m to nearly 1 km above the surface of the earth (Maldonado-Ramirez *et al.*, 2005). However, few definite facts exist with regard to how many fungi are dispersed and over what distances. Early studies on the aerial distribution of fungi suggested that distances of around 300 km were possible, although since then clouds of *Cladosporium* spores presumed to have originated in England have been tracked across the North Sea to the Danish coast, a distance of some 650 km (Carlile *et al.*, 2001). Aerial dispersion has been most studied for plant pathogenic fungi, and was reviewed in this context by Malloch & Blackwell (1992).

The number of spores that could potentially be transported by air movements is very large. Sanderson (2005) reported that a single fruiting body of *Ganoderma boninense* released around 2×10^6 basidiospores into the atmosphere per day. Fungi that fruit for limited periods also produce large numbers of spores, and a single *Coprinus comatus* that fruits for only 48 h has been estimated to produce around 5×10^9 spores in that time (Spooner & Roberts, 2005).

Numbers of fungal spores in an air sample will be dependant on many different factors including season, weather, height and possibly time of day. Figures of 3×10^4–2×10^6 spores m^{-3} have been reported (Carlile *et al.*, 2001; Spooner & Roberts, 2005). The number of fungal propagules in the air is also dependent on the height within the air column above the ground. At distances close to the ground (a few centimetres), there is generally little air movement or uplift due to laminar air, and so aerial dispersion would not be a major factor. However, once above this layer, dispersal increases rapidly and the value of 3×10^4–2×10^6 spores m^{-3} mentioned above was measured at a height of 1.5 m. Hence, it is to be expected that spores associated with raised fruit bodies, vegetation or insects and birds would be more likely to be widely dispersed (Spooner & Roberts, 2005). In general terms, the number of spores in the atmosphere decreases logarithmically with height, and a figure of 3 spores m^{-3} has been reported as a general value for air sampled at > 3000 m (Spooner & Roberts, 2005).

A major consideration in airborne dispersal of fungi in the Antarctic is the low levels of airborne particles in Antarctic air. In contrast to the estimates from temperate systems, counts of total CFUs (bacteria and fungi) or spore propagules (fungi and others) in low-altitude air systems are of the order of 0.5–3 m^{-3} (Marshall, 1996a). Marshall (1996a, b) and Chalmers *et al.* (1996) identified fungi from air sampling at Signy Island, *c.* 700 km from the continental Antarctic, and identified a number of species commonly encountered in airborne samples, particularly chlamydospores and spores of *Cladosporium* spp. A considerable limitation in determining the extent and significance of airborne dispersal by fungi is the limited amount of information available on the numbers and types of fungi present. To date, some 1000 named fungal species have been recorded from the general Antarctic/sub-Antarctic area, with some 500+ of these being described from the maritime and continental Antarctic (Bridge *et al.*, 2008a). Many fungi will not grow easily on standard mycological media, and so many groups (such as the *Entomophthorales*) that usually require specific isolation methods are unlikely to be recorded accurately. A large proportion of the 900 reported species are considered to be dispersed primarily through the air, with the majority being conidial ascomycetes. In general, few groups that are normally soil- or waterborne are present in any great number (Bridge *et al.*, 2008b). Where usually soilborne species have been recorded, they are often present in large numbers.

In general terms, most fungi do not have particular geographic distribution patterns, although many species that are associated with particular plants or animals will only occur where such associations are present (e.g. *Termitomyces* species associated with termite mounds). The presence in the Antarctic of fungi pathogenic to plants and invertebrates not found there suggests dispersion from other regions. A number of fungi fall into this category, and one particular example is an isolate of *Lecanicillium* sp. This genus is commonly found in tropical and temperate regions as an invertebrate pathogen, particularly on *Coleoptera*. The genus has been isolated from the Antarctic on a number of occasions, where it has been found in soil (Onofri *et al.*, 2000; Tosi *et al.*, 2002), and it has also been reported to form an active association where fungal growth was observed with algae and bacteria in an endolithic community (Hughes & Lawley, 2003). Current molecular analysis of the isolate from the endolithic community suggests that it is very similar to, but possibly distinct from, the insect-associated species of *Lecanicillium lecanii*, *Lecanicillium muscarium* and *Lecanicillium longisporum* (P.D. Bridge, unpublished data). A second example of a fungus adopting an alternative lifestyle is *Rhizoscyphus ericae*. This species is normally found as a mycorrhizal associate of ericoid plants. In the Antarctic, it has been isolated exclusively from the rhizoids of the liverwort *Cephaloziella* (Chambers *et al.*, 1999). Molecular work with these isolates has confirmed their relationship to temperate and Northern hemisphere isolates (Chambers *et al.*, 1999).

Other fungi that are normally associated with particular hosts, such as *Beauveria bassiana* (Göttlich *et al.*, 2003), have been found in Antarctic systems where their hosts are absent, and other species such as most of the nematophagous fungi represent common cosmopolitan species, but occur in the Antarctic on endemic hosts (Gray & Lewis-Smith, 1984). Recent, or continual colonization, is suggested by the small proportion ($< 10\%$) of recorded fungi that have been considered unique to the Antarctic; this compares with the almost 100% endemism within the region reported for other nonaerial dispersed groups such as nematodes and many invertebrates.

Bacterial dispersal over Antarctica has been much less well documented. Aerosol bacteria studied over the southern ocean during the aerosol characterization experiment 1 were found to be present in samples from altitudes as high as 5.4 km. The estimated ratio of bacteria to the dominant aerosol particle, sea salt, was found to vary, but averaged about 1% (Pósfai *et al.*, 2003). Prokaryotic biodiversity in air samples collected at Rothera Point (Adelaide Island, Antarctic Peninsula) was examined using PCR-based molecular techniques (Hughes *et al.*, 2004). The rRNA gene sequences from a range of microorganisms were recovered, including cyanobacteria, actinomycetes, diatom plasmids, uncultivated and unidentified bacterial groups. The closest matches for many of the 16S rRNA sequences obtained were sequences previously recovered from the Antarctic (including Antarctic soil, marine and lichen genera) or from other cold environments. These results suggest that much of the aerobiota was of regional origin. Air-mass-back trajectory

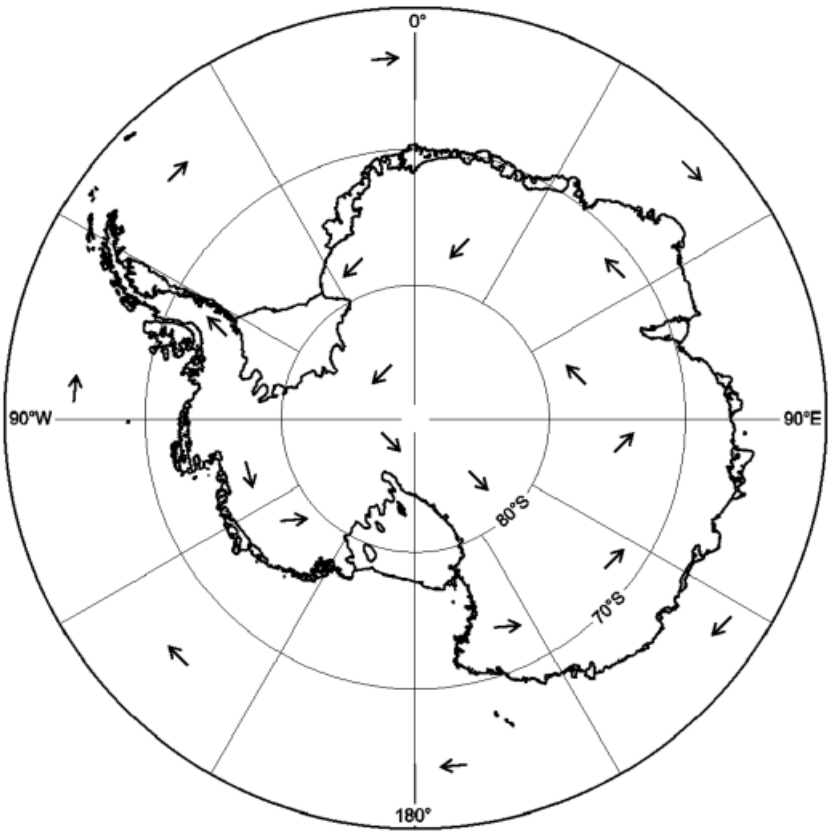

Fig. 4. Prevailing wind movements over the continent during the Antarctic winter (not to scale).

data (Kottmeier & Fay, 1998) collected during the sampling period suggested that the sampled air might have travelled over the Antarctic Peninsula and Weddell Sea before reaching Rothera Point. As a result, a proportion of the detected aerobiota may have been transported from distant Antarctic sites. However, prevailing wind patterns across the Antarctic suggest that much of the material present in the air is derived from the continent itself (Fig. 4). Data on large-scale transport of biological particles is scarce, although Brown & Hovmøller (2002) did discuss the aerial dispersal of pathogens over distances of 500 km or more on global and continental scales. They showed that long-distance dispersal of fungal spores by the wind can spread plant diseases across and even between continents and also re-establish diseases in areas where host plants are seasonally absent. Prospero *et al.* (2002) demonstrated the large-scale distribution of dust around the globe (which is likely to have associated biological material). They showed that the largest and most persistent sources of atmospheric dust are located in the Northern Hemisphere, mainly in a broad 'dust belt' that extends from the west coast of North Africa, over the Middle East, Central and South Asia, to China. They found remarkably little large-scale dust activity outside this region.

There are numerous fungi that appear to have a bipolar distribution, including around 20 lichen-forming species and basidiomycetous yeasts (e.g. Galloway & Aptroot, 1995; Vishniac & Onofri, 2003). Bridge *et al.* (2008b) found that internal transcribed spacer sequences for an Antarctic *Pythium* sp. were identical to those from Arctic collections, and Upson *et al.* (2007) found rRNA introns in some Antarctic isolates of *R. ericae* that were similar to introns found in isolates from other geographical regions. These findings could suggest globally dispersed populations; however, to date, only a limited number of comparisons of potential molecular markers for fungi from the Arctic and Antarctic have been conducted, and so it is not possible to assess whether the isolates from different locations represent globally dispersed organisms or geographically isolated populations that have diverged allopatrically.

Colonization

Microbial colonization in time and space is a function of emigration, immigration, growth and death. In addition, adaptations that enhance survival in air are similar to those that make microorganisms suitable for Antarctic colonization. The colonization success of propagules undergoing airborne transport to Antarctica depends upon the following factors: (1) survival during aerobiological transfer, (2) the physiological and biochemical capacities of propagules

on deposition and (3) habitat conditions. However, very little is currently known about the aerial transport of microorganisms, plants and animals into and between Antarctic terrestrial and freshwater habitats, although in the few studies that have been conducted (Marshall, 1996a; Hughes *et al.*, 2004), propagule abundance and diversity in the air are low. Habitat affects colonization success because the potential and viability of a propagule must match a favourable habitat for settlement, growth and establishment, with adequate time for establishment before conditions become unfavourable.

There are two main barriers to colonization of Antarctica by airborne species; the remoteness of Antarctica and the associated difficulty in dispersal and the inhospitable conditions that make survival and establishment difficult. In the last 100 years, these barriers have been eroded. Firstly, increasing human presence in the Antarctic, either due to tourism or due to establishment of new Antarctic bases by national operators, has made it easier for microorganisms from all over the world to gain access to Antarctic terrestrial and marine environments. Secondly, the onset of regional climate change on the Antarctic Peninsula has resulted in an increase in the temperature of almost 3 °C in the last 50 years. The Peninsula is not only warmer, but there is greater availability of liquid water in some locations, due to ice and snowmelt and an increase in the frequency of rain, rather than snow (Convey, 2001). Increased precipitation makes the dispersal and increased temperature the establishment of alien microorganisms more likely.

The Antarctic and sub-Antarctic environment has a diverse range of organisms that coexist in many unique interactions. This ecology is susceptible to introduction of invasive alien species, from fungal pathogens of native plant species to bacteria and viruses that may cause disease in seabird and marine mammal populations (Frenot *et al.*, 2005).

Anthropogenic factors

A key source of airborne inoculation in Antarctica is human activity. Since man first arrived in the Antarctic he has brought non-native microorganisms with him. For example, materials, including pony dung, found at camps erected by early Antarctic expeditions led by Scott and Shackleton, were found to contain viable *Bacillus* and *Micromonospora* spp. after 80–90 years in the polar environment (Nedwell *et al.*, 1994). Even the most remote areas of Antarctica have been contaminated by human presence. When Mount Howe in the La Gorce Mountains (87°21′S, 149°18′W; 330 km from the South Pole) was first visited in 1971, spores of a *Penicillium* sp. were accidentally released when mouldy food was opened (Cameron, 1972).

Attempts to detect human commensals deposited from the air around Antarctic research stations have yielded mixed results. Using culture-dependent and PCR techniques, Upton *et al.* (1997) failed to culture human commensals from around Halley Research Station (which is situated on a floating ice shelf). However, Sjöling & Cowan (2000) did find evidence of long-term persistence of *Escherichia coli* DNA at an abandoned field camp using species-specific DNA primers. Examination of fungal biodiversity in soils from pristine and human-impacted sites in Eastern Antarctica using culture techniques showed that 12 taxa were restricted to soils from near the Australian Casey Station and suggests significant introduction of fungal species by human activities (Azim & Seppelt, 1998).

The majority of coastal Antarctic stations dispose of sewage waste, and its associated non-native microbial species, by releasing it into the sea with maceration as the only treatment. This may cause microbial contamination of marine invertebrates, fish, seabird and seals. A study of aerial distribution of sewage microorganisms from an Antarctic sewage outfall showed that faecal coliforms were killed rapidly by desiccation and UV stresses present in the Antarctic environment (Hughes, 2003). Recent measures to reduce alien microbial species released into the near-shore marine and aerial environments have been the installation of the sewage treatment plants at, for example, Rothera Research Station (UK), Scott Base (NZ) and McMurdo Station (USA). Improved sewage treatment has dramatically reduced the input of non-native human gut bacteria into the Antarctic environment (Hughes, 2004).

Life at the edge

Microorganisms in ice

To date, studies of life in remote icy environments have generated a huge range of estimates of microbial numbers (Table 2), and increasingly, estimates of activity and impact are starting to be generated. These microorganisms represent a significant carbon pool. The implication of aerial transport for future studies of such icy environments is that it is essential to know how quickly they are accumulated (growth rate vs. input rate), i.e. whether the microorganisms identified are merely transient organisms, established but not dividing, established and dividing slowly or established and reproducing effectively.

Microorganisms in the exosphere

The challenges and stresses faced by microorganisms in aerial environments could be considered a continuum, where the severity of the environment increases with altitude. Viable microorganisms have been obtained from the upper atmosphere and have also been launched into the Earth's orbit in an attempt to study their survival outside the atmosphere (Wainwright *et al.*, 2003). Although isolates from the

Table 2. Estimates of total population density of microorganisms in icy environments

Number	Location	Reference
< 1 CFU mL^{-1}	Polar ice	Abyzov *et al.* (1982)
1–5 CFU mL^{-1}	Glacial ice Canadian High Arctic	Dancer *et al.* (1997)
10–50 cells mL^{-1}	Meltwater	Bulat *et al.* (2004)
$2–3 \times 10^2$ cells mL^{-1}	Melted ice	Karl *et al.* (1999)
2.8×10^3 and 3.6×10^4 cell mL^{-1}	Melted ice	Priscu *et al.* (1999)
2×10^4 cells mL^{-1}	Aeolian deposition in Greenland	Tung *et al.* (2005)
6.6×10^4–3.7×10^5 cells mL^{-1}	Snowmelt, ice marginal and subglacial streams	Skidmore *et al.* (2005)
6×10^7 cells mL^{-1}	Greenland ice core	Sheridan *et al.* (2003)
10^7 cells g^{-1}	Sediment beneath Antarctic ice	Lanoil *et al.* (2009)

stratosphere have been recognized as modern bacteria from Earth (i.e. S*taphylococcus*, *Bacillus*) (Narlikar *et al.*, 2003), a minuscule survival rate of freeze-dried bacteria in space is all that would be needed to permit the movement of microbial life outside the atmosphere. The experiments of Horneck & Rettberg (2002) have shown that bacteria could survive space travel, including lift off from the place of origin and re-entry into a planetary atmosphere. It has been shown that the Gram-positive, spore-forming organism, *Bacillus subtilis*, can survive for 6 years in space with some of the original population remaining viable after their recovery (Horneck, 1993), and they can survive an atmospheric entry velocity of 1.2 km s^{-1} in a basalt rock attached to a sounding rocket (Fajardo-Cavaros *et al.*, 2005). Despite the general opinion that small particles get burnt by frictional heating during entry into the stratosphere, there might be ways to permit intact injection, as suggested by Wainwright *et al.* (2003), where microbial life could be transported in connection with comet dust. Hence, the potential for transfer into and out of the atmosphere has been studied. Cockell *et al.* (2007) launched a cryptoendolithic habitat, made of a gneissic impactite inoculated with *Chroococcidiopsis* sp., into the Earth's orbit. After orbiting the Earth for 16 days, the rock entered the Earth's atmosphere and was recovered in Kazakhstan. The heat of entry ablated and heated the original rock to a temperature well above the upper temperature limit for life, and also to below the depth at which light levels are insufficient for photosynthetic organisms (*c.* 5 mm), thus killing all of its photosynthetic inhabitants. This experiment showed that atmospheric transit acts as a strong biogeographical dispersal filter to the interplanetary transfer of photosynthesis. However, studying adaptations for the aerial transport of microorganisms might help in the search for microbial life on other planets.

Airborne microorganisms and climate change

Environmental factors have an important role in determining the prevalence of airborne microorganisms. Environmental factors that influence airborne microbiota include wind speed, wind direction, RH, temperature (Fig. 3), exposure to UV light and solar radiation, cloud and fog, but also chemicals present in the air and air pollutants. Seasonal climatic factors also play a role, including the time of day, type of vegetation present, agricultural, industrial and other human activities. The time over which these parameters operate is another important factor.

Often, environmental factors act in combination; for example, numbers of airborne bacteria increase with temperature and wind velocity (Harrison *et al.*, 2005) whereas airborne fungi increase in number with temperature (Seino *et al.*, 2005), although these effects are variable. The density of microorganisms in the air can also be affected by their method of release from contaminated surfaces, which includes factors influencing their aerosolization, such as air velocity, colony structure, moisture conditions, vibration of the surface and time (Gorny, 2004). Prospero *et al.* (2005) found that microorganism and dust concentrations were unusually great in 1997, possibly in response to the strong El Niño, which suggested that the long-range transport of microorganisms might be particularly responsive to climate variability in general. Elsewhere, RH can affect the UV-induced inactivation of airborne bacteria (Peccia *et al.*, 2001), and solar radiation can inactivate airborne bacteria at both moderate (50–60%) and high (85–95%) levels of RH, but these inactivation rates are greatest at moderate RH levels (Paez-Rubio & Peccia, 2005). In addition, solar radiation has marked differential lethal effects depending on the accumulated total solar irradiance, solar spectral property, bacterial species composition and bacterial laden particle size – for each micrometre increase in particle diameter, there was an almost 11% increase in survival up to at least 7-μm-diameter particles (Tong & Lighthart, 1998). Such effects may operate at the level of individual microenvironments, a fact often overlooked.

Growing evidence suggests that climate change is a result of anthropogenic activities including the release of greenhouse gases. Few places on Earth have been affected by climate change more than the Antarctic Peninsula, which has experienced a dramatic increase in annual average temperatures of almost 3 °C over the last 50 years (Hansen

et al., 1999). Consequences of this include sudden ice shelf retreat, deglaciation, reduction in snow cover and increased precipitation over the Peninsula. Increased temperature and water availability has significantly increased the duration of the growing season for terrestrial Antarctica biota. Long-term studies show an increase in the abundance and distribution of both *D. antarctica* and *C. quitensis* in the Peninsula over the last 25 years (Smith, 1994). Rapid expansion of bryophyte ground coverage has been observed in the maritime Antarctic (Smith, 1990), and field manipulations confirm that warming may have widespread effects on terrestrial ecosystems. However, currently, Antarctic summer temperatures are likely to be near or below minimum threshold temperatures for many physiological processes of potential colonists. Although even a minor change in physical conditions associated with climate change may allow successful colonization, which in turn may impact on existing ecosystems.

Convey (1996) predicted that climate change may lead to 'an increase in rate of colonization by species new to the Antarctic, thereby increasing diversity, biomass, trophic complexity and habitat structure, with possible loss of existing Antarctic species and communities through increased competition'. Colonization events in the terrestrial Antarctic environment are likely to be infrequent, because sites with appropriate physical and microclimate characteristics suitable for colonization are rare, isolated and often surrounded by large areas of snow, ice or ocean. Winds are dominant agents of biological transport between terrestrial sites as they can transport particles over long distances. In possibly the most comprehensive Antarctic aerobiological study to date, Marshall (1996a, b) showed that cyclones moving around the continent were associated with a dramatic influx of airborne biological material into the South Orkney Islands from South America. Crude estimates suggested that suitable weather patterns occurred with a mean annual frequency of 1.5; however, less dramatic influxes of biological material are likely to be more common. At continental sites, katabatic winds flowing off the high continental plateau towards the coast may inhibit local aerobiological transfer of propagules towards inland sites. However, as yet, little evidence exists to support this. Nevertheless, markers of long-distance propagule transfer do include the occurrence of exotic pollen trapped in moss cushions (Linskens *et al*., 1993) and exotic plants on volcanically warmed soils in both continental and maritime Antarctica (Convey *et al*., 2000). Recently, it has been hypothesized that marine algae and bacteria induce water condensation and ice nucleation in order to improve their dispersal and transport in the atmosphere. Thus, they influence not only distance and destination of the journey but also the world climate (Hamilton & Lenton, 1998), making this highly relevant for future scenarios in climate change.

Summary

From the limited number of studies available to date, it is clear that the input of airborne microorganisms into Antarctica does indeed influence the microbial biodiversity present. However, to our knowledge, there are no existing long-term studies of microbial colonization processes in Antarctica. With the relative isolation of the Antarctic continent and the climate of the Antarctic Peninsula warming faster than anywhere else on Earth, this represents a unique opportunity to try to understand the effects of changes in microbial biodiversity on biogeochemical cycling and ecosystem function.

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