Review

# Non-indigenous microorganisms in the Antarctic: assessing the risks

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**The Antarctic continent is frequently cited as the last pristine continent on Earth. However, this view is misleading for several reasons. First, there has been a rapid increase in visitors to Antarctica, with large increases at research bases and their environs and to sites of major tourist interest (e.g. historical sites and concentrations of megafauna). Second, although substantial efforts are made to avoid physical disturbance and contamination by chemical, human and other wastes at these sites, little has been done to prevent the introduction of non-indigenous microorganisms. Here, we analyse the extent and significance of anthropogenic introduction of microbial 'contaminants' to the Antarctic continent. We conclude that such processes are unlikely to have any immediate gross impact on microbiological community structure or function, but that increased efforts are required to protect the unique ecosystems of Antarctica from microbial and genetic contamination and homogenisation.**

## Human impacts on Antarctica

The Antarctic Continent is often described as the last pristine continent on Earth, where the combination of geographic isolation, environmental extremes and limited accessibility have restricted both the direct impact of human activities (in terms of the numbers and duration of human presence on the continent) and the consequences of these impacts. Human presence on the continent spans a mere 190 years, following the first documented landing in 1820. Since that time, human colonisation has followed a pseudo-exponential increase, with a transition from economic exploitation (sealing, whaling and fishing) and heroic exploration to modern scientific investigation and tourism [1–4]. The dramatic rise in the numbers of visitors to the continent over the past three decades corresponds in part with a growing international interest in Antarctica as a laboratory for multidisciplinary research. Although visitor numbers have been dominated numerically by Antarctic ecotourists [1,2,4], in reality staff working with national research programme operators spend ca. 20 times more time, cumulatively, on the Antarctic continent than those associated with the tourist industry [5].

The impacts of scientific and tourist activities take many forms [2], but are generally similar to those occurring elsewhere on the globe [6], although to a lesser extent. Impacts can include physical damage, chemical and biological contamination, biological invasions and resource overexploitation. Although the specific nature and extent of these impacts have been comprehensively reviewed [1,3,7–10], most attention, in the case of biological invasions, has focussed on processes involving higher organisms (such as plants vertebrates and macroinvertebrates) [1,11,12], with less consideration of the significance of microbial contamination. Where microbial introductions have been addressed, the focus has been largely restricted to the impacts of human and animal pathogens (including viruses) [7,8,13] and organisms with deleterious implications (such as the non-indigenous fungal deterioration of timbers in historic huts [14]). Much less attention has been given to other forms of microbial contamination (but see [15,16]). In this review, we focus specifically on the processes and consequences of microbial contamination and invasions on Antarctic microbiota, particularly those mediated by human activities on the continent.

## The concept of impact

For larger organisms, such as plants, impact of a given alien species can be defined as the product of its range size, abundance per unit area and effect per individual or unit biomass [17]. To assess overall impacts of alien species in an area, the 'per species' level impact can be multiplied by the number of such species [18,19]. Making such assessments for microbes is clearly difficult [20]. Therefore, another measure of impact is required. Propagule pressure, or the number or frequency of individuals introduced to an area, and colonisation pressure, or the numbers of taxa introduced to an area per unit time, have proven effective predictors of the numbers and status of alien organisms in higher taxa [21]. For microbes these variables might also be difficult to quantify [21]. However, in many other taxa, strong relationships exist between human activity and both propagule and colonisation

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**Table 1. Specific annual impact values for Antarctica and other regions**

| Location/date | Land area ($km^2$) | Annual impact[a] | Specific annual impact[b] | Relative specific impact |
|---|---|---|---|---|
| Antarctica (total), 1880 | $1.4 \times 10^7$ | 0 | 0 | 0 |
| Antarctica (total), 1903 | $1.4 \times 10^7$ | $35 \times 1$ | $5 \times 10^{-6}$ | 0.0001 |
| Antarctica (total), 2009 | $1.4 \times 10^7$ | $34\,000 \times 0.1$ | $1 \times 10^{-4}$ | 0.02 |
| Antarctica (ice-free[c]), 2009 | $4.5 \times 10^4$ | $34\,000 \times 0.1$ | $5 \times 10^{-3}$ | 1 |
| Marion Island, 2009[d] | 290 | $80 \times 0.08 + 16 \times 1$ | $7.7 \times 10^{-2}$ | 15 |
| New Zealand, 2010[e] | $2.7 \times 10^5$ | $4.4 \times 10^6 \times 0.9$ | 14.7 | 2930 |
| Deception Island, 2006/2007[f] | 0.5 | $16\,800 \times 4.6 \times 10^{-4}$ | 15.5 | 3090 |
| China, 2000[g] | $9.6 \times 10^6$ | $1.24 \times 10^9 \times 0.9$ | 115.8 | 23 150 |
| McMurdo Station, 1997[h] | 0.5 | $1258 \times 0.2 + 100 \times 1$ | 703 | 140 640 |
| Greater London, UK, 2009[i] | 1572 | $7.75 \times 10^6 \times 0.9$ | 4437 | 887 404 |

[a] Annual impact is defined as the total number of personnel multiplied by the fractional occupancy (the estimated proportion of the year spent occupying the specified region). For national or urban sites, this value is arbitrarily set at 0.9 (i.e. on average members of the population occupy the region for 90% of each year). For Antarctic visitors, fractional occupancy is set at 0.1 [averaging short occupancy (tourists) and long occupancy (scientists and support staff)].

[b] Specific annual impact is calculated as the annual impact divided by the terrestrial land area ($km^2$). Relative specific impact is relative to Antarctica (2009), defined as 1.

[c] Ice-free land area of the Antarctic continent: 0.32% of total.

[d] Marion Island is one of the sub-Antarctic islands that form associated and dependent ecosystems of Antarctica [11].

[e] Data from www.stats.gov.nz.

[f] Sub-Antarctic Deception Island is one of the top 'Antarctic' ecotourism sites.

[g] Data from www.cia.gov.

[h] Data from www.nsf.gov.

[i] Data from www.statistics.gov.uk/.

pressure, both in the Antarctic region and elsewhere [22,23]. Therefore, as some measure of the probable impact of microbial organisms, the extent of human activity can be used. This measure is relatively simplistic; one obvious caveat being that all activities are not equal. For instance, although ca. 16 000 tourists visit Whalers Bay (Deception Island, one of the most popular tourist sites in Antarctica) in a season, their microbial input is probably less than that of a small research station which can receive considerable amounts of cargo, fresh foods, building supplies and other materials in a season.

Here, we refer to such human activity as 'anthropogenic impact' (in terms of disseminating non-indigenous microorganisms into the immediate environment) and define it as the integrated value of all individuals' presence at a location (which might be a single place or an entire continent) in any specific year (a single individual present at a site for an entire year would yield a value of 1, and one present for three months 0.25). We also define 'specific impact' by dividing this value by the total land area available, as an approximate measure of the degree of anthropogenic impact on a defined region as a whole. Although an estimation of the cumulative duration of human presence at any site is actually a measure of 'introduction potential', we argue that the anthropogenic transport and dissemination of microorganisms is an inevitable consequence of human presence.

This approach can be refined by identifying specific environmental domains at incremental spatial scales. We acknowledge that this calculation will tend to generalise the impact across the defined area, and we readily acknowledge that microbial dispersal, whether in cities or ice-free valleys of Antarctica, is by no means homogeneous. Nevertheless, we argue that this approximation provides a useful comparative determinant for visualising the likelihood of human impacts in regions where the consequences of such impact may be of ecological concern.

An initial comparison of the calculated specific impact values (Table 1) suggests that, although the value for the entire Antarctic continent is extremely low, values rise by factors of 50 and 2 million when calculated for the ice-free areas of the continent or for the US McMurdo Station on Ross Island, respectively. This is particularly important because human occupancy of the Antarctic continent is largely concentrated in ice-free areas, on which most of the government-operated scientific research stations are sited and where the terrestrial tourist landings (at historic sites and concentrations of the 'charismatic megafauna') are found [2].

Some of the consequences of human impact are readily quantifiable and well documented. For example, all sites of habitation (principally scientific stations, but also field camps and even historic exploration relics) have measurable waste outputs. A proportion of these outputs, typically the aqueous fractions, are released to the local marine environment via submarine outflow pipes [24,25]. Other human impact effects, such as disturbance of animal and bird populations, are well documented (see reviews [1,2]).

## Inputs of non-indigenous microorganisms

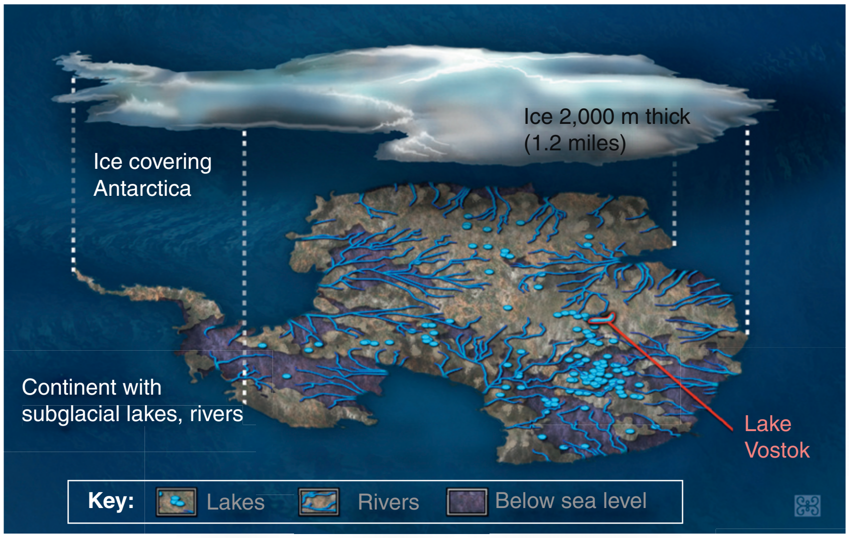
Despite its geographical isolation, the Antarctic continent is not and has never been microbiologically isolated, but is constantly seeded by populations of non-indigenous microorganisms transported from the southern hemisphere continents by high altitude aeolian processes [26,27]. No quantitative estimates of the total inorganic (or organic) inputs to the Antarctic continent are available, but the annual volume is expected to be very large. Whatever the scale, the numerical values for input of non-indigenous microorganisms should be considered in the context of the extant microbial cell occupancy, estimated for Antarctic Dry Valley soils as $10^6$–$10^8$ g [28], or equivalent to $10^{10}$–$10^{12}$ cells for a 1-$m^2$ × 1-cm deep soil profile. Our hypothesis, although as yet untested, is that the extent

### Box 1. The Lake Vostok issue: endemism and contamination

The invasion of non-indigenous microbes into Antarctica is an especially important issue for the exploration and stewardship of Antarctic Subglacial Aquatic Environments (SAEs). The largest of these liquid water environments, Lake Vostok, lies 4 km beneath the surface of the ice and was detected by airborne ice-penetrating radar surveys in the 1970s. Later observations showed that it has a maximum water depth of ca. 1000 m, and area of 15 690 km$^2$, making it one of the world's great lakes. Lake Vostok occupies a rift valley, and is likely to have formed 15–25 million years ago, with replacement of its water at a timescale of thousands of years by melting and refreezing of the overlying ice. More recent surveys have shown that the subglacial Antarctic environment is composed of vast watersheds of many interconnected lakes, thin films of liquid water and flowing rivers and streams [78].

There is intense interest in Lake Vostok and other SAEs as potential habitats for microbial communities, particularly given their long history of isolation under extreme pressures and other unusual environmental conditions. There is also much concern about potential contamination of these unique environments, perhaps the last pristine waters on Earth, by non-indigenous microbes during any attempts to explore them [79]. In 1998, a Russian ice-drilling project at Vostok Station penetrated to 3623 m depth, some 120 m short of breaking through into the liquid fresh water of subglacial Lake Vostok. The drill penetrated into accretion ice (ice that has thawed and refrozen) but drilling was terminated to avoid contamination of the 'pristine' Lake Vostok water (Figure I).

Concerns have been heightened by analyses of the drilling fluids used to fill the borehole, which showed a large number of contaminant microbial taxa [80]. The potential introduction of microbial and other contaminants has generated controversy over the origin of microbes detected in Lake Vostok lake ice, and has underscored the need to minimise or eliminate such contamination to reliably assess the native microflora (if present) of the lake, as well as to prevent the introduction of taxa that could survive or grow under these extreme conditions. An initial set of guidelines for the long-term stewardship of these waters [81] recognised that the interconnectivity of the SAEs increased the risk of spreading any such microbial cell and nucleic acid contamination. These guidelines were subsequently refined by the Scientific Committee for Antarctic Research, culminating in an international code of conduct for SAE exploration and research. This code includes principles and guidelines that explicitly address the risk of introduction of non-indigenous microorganisms into Antarctic subglacial waters [82].



TRENDS in Microbiology

**Figure I.** Subglacial lakes and rivers on the Antarctic continent.

of the physiological, genetic and ecological impacts of introduced microorganisms on extant microbial communities is to some extent a function of the numerical ratio between introduced organisms and extant organisms.

Aeolian particle capture experiments have demonstrated that the majority of transported microorganisms are of regional origin [26], but the fact that some species show a clear bipolar distribution (e.g. [29]) suggests that both aeolian capture and transport processes could also operate globally. The efficacy of the aeolian transport route for microscopic propagules is also illustrated by the exceptional bryophyte communities found around widely separated areas of geothermally active ground in Victoria Land, the South Shetland Islands and South Orkney Islands [30], which also illustrate the requirement for suitable habitat for colonisation as well as the ability to disperse *per se*. Somewhat surprisingly, some airborne particle traps have shown little evidence of marine microbial phylotypes in terrestrial ice-free areas [31]. Given the propensity of the southern oceans to generate aerosols, which would be obvious vehicles for transport of marine microorganisms, and clear evidence of marine aerosol nutrient input to near-coastal terrestrial ecosystems in the maritime Antarctic [32], this remains something of an anomaly.

The continental surface is continuously exposed to natural seeding by inorganic and organic particles. However, the discovery of subglacial lakes that may have been physically and genetically isolated for millions of years (Box 1) has raised the possibility that unusual microbiota may have evolved in these waters and are sequestered beneath the ice sheet. This discovery has also raised concerns about the vulnerability of such lakes to microbial contamination.

The concept of anthropogenic microbial contamination of the Antarctic environment has been considered for some time (reviewed in [33]), but has largely focussed on

### Box 2. Anthropic microbial contamination of field camps sites

As a measure of potential impact, and based on the values calculated here of daily microbial dissemination, it is possible to roughly estimate the local microbial contamination impact for a field party working in a controlled and localised camp for a given period. For a typical example, where six individuals occupy a field camp location of 50 $m^2$ (Figure I) for a period of 10 days, the cumulative microbial impact is ca. $6 \times 10^{10}$ cells. Assuming that these cells were evenly distributed into the top 1 cm of the mineral soil of the camp site (which constitutes a ca. $5 \times 10^5$ $cm^3$ volume), each 1 $cm^3$ volume would receive around $10^5$ cells, equivalent to between 0.1% and 10% of the natural microbial load in such soils [34].


TRENDS in Microbiology

**Figure I.** A typical Antarctic Dry Valley field camp. A 'corral' system is used to ensure that physical (and biological) impact is limited to the interior of the site.

contamination of soil and water by the effluent streams of scientific stations. Numerous studies have demonstrated the presence of both culturable coliforms and other human faecal bacteria [24] and *Escherichia coli* phylotypic signals [34] in the vicinity of research stations and their effluent outfalls. These sources of contamination are highly localised and might be of more significance to inshore marine habitats than terrestrial environments because many research stations are positioned on the coast and discharge human waste directly into the sea.

More recently, and in line with a dramatic increase in tourist access to the Antarctic continent, awareness of anthropic dissemination of microorganisms into Antarctic terrestrial ecosystems has been growing [27]. The surface of the human body typically supports a population of over $10^{12}$ microorganisms [35]. These organisms are continually released through the direct and unavoidable processes of hair loss, skin cell sloughing, sneezing, coughing, etc. If we conservatively assume that the daily body surface turnover is 0.1% (human epidermal cell turnover is estimated at around 28 days [36]), this is equivalent to a daily personal dissemination to the immediate environment of the order of $10^9$ microbial cells. This value does not represent a particularly large carbon contribution to the environment, but it potentially represents a significant input of novel genetic elements (Box 2).

Contamination by non-indigenous microorganisms might also be an indirect consequence of human activities; that is, derived from the many elements of the physical infrastructure which support activities in the Antarctic, such as clothing, equipment and foodstuffs. Although there might be considerable overlap in microbial populations disseminated by these direct and indirect mechanisms, the technical issues of decontamination are clearly very different. An example of an indirect mechanism of contamination is the 132 kg of soil containing viable fungi and bacteria from the Falkland Islands and South Georgia that was transported into the Rothera Research Station (UK) on uncleaned vehicles [10]. Self-regulated 'codes of conduct', which guide the behaviour of both the Antarctic tour operators and Antarctic national research activities, are designed to prevent gross contamination (through cleaning of footwear, clothing, packs and other equipment). However, the efficacy of these codes of conduct varies widely amongst nations and categories of visitors to the continent [27], as evidenced by ongoing calls for more uniform implementation of the formal requirements of the Environmental Protocol to the Antarctic Treaty [37], and substantial differences in seed propagule load amongst visitor categories [38].

## Distribution and dissemination

The majority of human activities on the Antarctic continent are focussed in highly localised areas, typically in and around scientific stations, field camps and historic and biologically important sites. It is therefore reasonable to assume that a large proportion of anthropogenic input contamination is localised to these sites. This is broadly supported by local contamination studies [39], although no extensive regional contamination studies have been

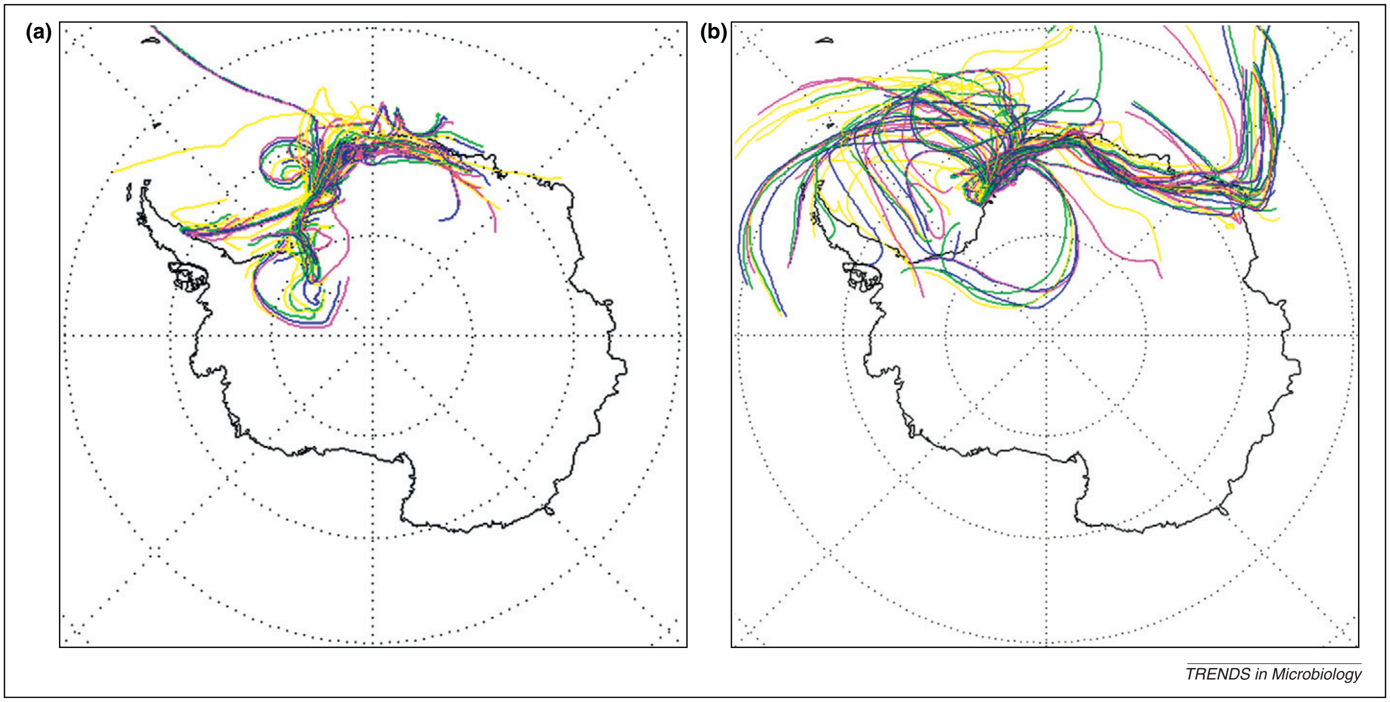


**Figure 1**. Fourteen day windflow backtrack patterns. **(a)** September to October 2004 and **(b)** January to February 2005. The patterns show extensive and highly variable air movements over west Antarctica (reproduced, with permission, from [31]).

reported. The impact of such localised contamination on the non-impacted (pristine) regions of the Antarctic continent is therefore dependent on 'natural' physical processes, most notably aeolian transport. The difficulty in determining whether a fungal species has been introduced is illustrated by *Aspergillus fumigatus*, which can cause aspergillosis in bird populations. This species was isolated from soil near Adélie penguin colonies at Cape Hallet, Victoria Land [40], but has also been detected in soil in a remote dry valley [41].

Although few studies have reported aeolian transport of non-indigenous microorganisms (but see [30]), the coastal regions of the continent are subject intermittently to very high velocity katabatic winds which transport, at least locally and periodically, high volumes of mineral fines and biological propagules [42]. Conversely, Antarctic air typically has only low levels of airborne particles [26]. It is therefore uncertain to what extent microbial contaminants resulting from human activities are disseminated, and whether these dissemination patterns occur on scales of metres or (many) kilometres. Studies have shown non-indigenous microbial signals in impacted sites but not from 'reasonably close pristine' sites [43], suggesting that transport might be local. Clearly, if wind-borne dissemination processes are significant, they would inevitably result in enormous 'dilution' of the contaminant signal, and dissemination processes which are dependent on prevailing wind flows will certainly not result in a homogeneous distribution. Backtrack trajectory analyses (see, e.g. [30]) might be relevant, as they demonstrate the extremely wide origins from which air masses affecting parts of Antarctica originate (Figure 1). Clearly, there is some conflict in the conclusions of these studies, suggesting that studies focussing on the dissemination of identifiable marker organisms would be highly informative.

## Survival and function of non-indigenous microbial cells

It is a reasonable assumption that most incident organisms, whether of aeolian or anthropogenic origin, will be mesophiles with cardinal growth temperatures of ca. 0 °C ($T_{\mathrm{min}}$) to 40 °C ($T_{\mathrm{max}}$). Nevertheless, for mesophilic organisms, metabolic activity would be limited in soil habitats where mean summer surface temperatures are less that 10 °C and mean annual temperatures can be as low as ca. −20 °C [44]. At least in the short term, non-indigenous organisms are unlikely to significantly contribute to any aspect of nutrient cycling, owing to their very low density and very low metabolic activities.

This argument notwithstanding, the temperatures of different microenvironments in terrestrial ice-free Antarctica are not homogeneous. During the austral summer period, microniches (soil surface, lithic, etc.) experience temperatures substantially above the local mean (e.g. [45]). In protected habitats, outgrowth by invasive macroorganisms has been noted: for example, the growth of non-indigenous grass species in sheltered microhabitats offered by buildings [1], and non-indigenous species are increasingly evident in more pristine sites [46]. When species become established (such as temperate grass species on the sub-Antarctic islands [1]), they can dominate both environments and biogeochemical processes (e.g. [47]). We argue that given appropriate environmental conditions, similar processes will occur with microbial populations. This has already been demonstrated, with the discovery of established populations of temperate fungi in the Ross Island historic huts [14].

Generally, the survival of non-indigenous microorganisms, however disseminated, is expected to be low. The lifestyle of most incident microorganisms is unlikely to be well suited to the more 'extreme' elements of the Antarctic terrestrial environment, but it should be noted that the

### Box 3. Growth ranges of extremophiles

Cold-loving microorganisms were originally classified into different physiological classes based on their cardinal growth temperatures [83]:

**Psychrophile**: $T_{\min} < 0$ °C, $T_{\text{opt}} \sim 15$ °C, $T_{\max} < 20$ °C.

**Psychrotroph**: $T_{\min} > 0$ °C, $T_{\text{opt}} < 25$ °C, $T_{\max} < 35$ °C. This term is generally out of favour, and preferred generic term for organisms derived from low temperature environments is 'psychrophile' [84]. The term 'trophic' pertains to a nutritional state and is not useful for stipulating the temperature an organism can tolerate.

**Psychrotolerant**: $T_{\min} < 0$ °C, $T_{\text{opt}} \sim 15$ °C, $T_{\max} < 25$ °C.

**Mesophile**: $T_{\min} < 0$ °C, $T_{\text{opt}} \sim 30$ °C–35 °C, $T_{\max} < 45$ °C.

To circumvent the inadequacies of this terminology, the terms 'eurypsychrophile' and 'stenopsychrophile' have been proposed [85]. The term stenopsychrophile (formerly 'true psychrophile') describes a microorganism with a restricted growth temperature range that cannot tolerate higher temperatures for growth. Eurypsychrophiles (formerly 'psychrotolerants' or 'psychrotrophs') are microorganisms that 'like' permanently cold environments but can tolerate a wide range of temperatures extending into the mesophilic range (i.e. 'mesotolerant' not 'psychrotolerant').

climates of the Antarctic Peninsula and even some of the coastal continental oases are relatively benign (as compared to the Dry Valleys, for example). However, extensive culture-dependent studies have shown that the most common soil microbial isolates are either psychrotrophs or psychrotolerant strains of mesophilic species (Box 3). True psychrophiles are relatively uncommon [48].

Although it is not clear which of the 'extreme' elements would have the greatest impact on cell survival, it is probable that the low temperatures, rapid freeze–thaw cycling, desiccation and oligotrophy typical of Antarctic terrestrial soil habitats [49] would be detrimental to microorganisms not adapted to such microenvironmental conditions. A limited number of studies of cell survival in Antarctic soils [43] suggest that the retention of viability (measured as culturability) from the time of dissemination is measured in days rather than weeks or months. It was noted [50] that faecal coliforms lost viability rapidly, but that sporulating *Clostridium* sp. and *Bacillus* sp. were viable after >30 years of freeze–thaw cycles on the Fossil Bluff dump site on Alexander Island (Antarctic Peninsula). We therefore believe that it is unlikely that microorganisms of anthropogenic origin will establish viable populations in Antarctic habitats.

## Residual biological signals and opportunities for lateral gene transfer

Even if the survival of viable microbial cells is relatively short, a general perception exists that nucleic acids (and therefore phylogenetic signals) will have a much longer half-life. This perception is largely based on the macroscopic conditions typical of the more extreme portions of the Antarctic terrestrial environment which are not dissimilar to those used in the laboratory for long-term storage of biological materials (i.e. desiccation and freezing, as elements of freeze-frying). The few studies that have addressed the matter suggest that naked double-stranded DNA is stable for long periods in cold desert soils (e.g. [39]).

The potential of prokaryotes to exchange genetic information through lateral gene transfer (LGT) is recognised as a major factor in their evolution. In bacteria, LGT occurs through transformation (uptake and incorporation of naked DNA), conjugation (cell contact-dependant DNA transfer) and transduction (transfer of bacterial host DNA to a recipient cell via a bacteriophage). Advances in high-throughput sequencing technologies have clearly shown that LGT is a common and widespread process, and that all prokaryote genomes contain major regions of genes acquired from other domains during their evolutionary history [51].

Temperate soil environments have been shown to be conducive to LGT [52,53], but the susceptibility of cells to LGT is determined by the physiological and biological features of the community, occurring at a frequency of $10^{-1}$ to $10^{-8}$ per prokaryotic cell [51].

In the complex non-aqueous communities which constitute Antarctic desert soils, LGT may be limited due to physical separation of adsorbed cells. However, aqueous microlayers on mineral surfaces could provide a mechanism for microbial mobility, uptake of released nucleic acids and cell–cell contact, resulting in LGT. Naked DNA concentrations can exceed 1 μg/g in soils [54] and might persist for prolonged periods, particularly under Antarctic conditions [39]. Considering that non-indigenous microorganisms are not likely to be metabolically active, natural transformation might be the predominant form of LGT in Antarctic soils. However, the specialised microniche communities (e.g. chasmolithic, endolithic and hypolithic [55]) might be considered hotspots for LGT, in that they provide microenvironmental conditions which favour microbial community survival and growth (e.g. increased water bioavailability; temperature and desiccation buffering [55]) which might also increase the frequency and efficiency of LGT.

To date, little evidence exists for LGT in Antarctic soil environments [56,57] and much remains to be understood about the impact that LGT from non-indigenous microorganisms would have on Antarctic microbial communities. Given the potential for gene exchange to occur across wide phylogenetic distances, LGT potentially has the capacity to profoundly affect the evolution of these communities through altering their structure, diversity, function and robustness [58]. However, even if LGT events were to occur in this environment, LTG is often deleterious to the cell [51,59], not all genes are transferred equally [60] and traits are only maintained under appropriate selection pressures. Genetic modules which are frequently transferred in terrestrial environments via LGT are those allowing adaptation to rapidly evolving biotic interactions. These include antibiotic resistance genes [61] and degradative genes and pathways in response to the release of xenobiotics or new secondary metabolites [62,63]. Certainly, there is evidence that introduced microorganisms have the capacity to accelerate the degradation of contaminating hydrocarbons in Antarctic soils [64]. Therefore the acquisition of new genetic capacities (e.g. by LGT) could have unexpected benefits to the Antarctic terrestrial environments. The extent to which these would be maintained, however, would be dependent on continued selective pressure.

## Impacts of microbial introductions

### *Microbial pathogens*

Pathogens, particularly viruses, represent a potential threat to indigenous species, irrespective of domain. The occurrence and distribution of phages in terrestrial Antarctic microbial communities, although very poorly understood, might be important as a regulator of microbial biomass, in a manner similar to that proposed for other microbially dominated habitats such as hot springs [65]. A recent study identified that an Antarctic lake supported a relatively diverse virome [66]. The extent to which invasive species could introduce phages with host specificities broad enough to infect indigenous microbial hosts is a concern and this might conceivably impact biomass and energy flow in these systems.

The growing global disquiet surrounding emerging infectious diseases also extends to Antarctica, in particular due to the rapid spread of pandemic influenza viruses in recent years. The threat to indigenous bird life (e.g. penguins, petrels and skuas) from infectious diseases is far from negligible and has long been a subject of concern (see [8]). The potential for impacts via direct introduction from anthropic sources is clearly worrying given the uniqueness of Antarctic bird life, but is also complicated by the tendency of many species to forage in southern continental areas (such as Patagonia) where they might be exposed to pathogens from human waste streams and thus introduce pathogens indirectly [8].

For plants (including lower plants such as mosses, which are widespread on the Antarctic continent) the situation has been much less carefully assessed, although the threat posed by potentially invasive fungal diseases is highly pertinent. As an example, *Fusarium graminearum* and *Muscicillium theobromae*, which can cause vascular wilts in many different plants worldwide, were recently introduced onto the Antarctic continent as contaminants of fresh foods [67]. The same study demonstrated that *Botryotinia fuckeliana* and a range of other microbial taxa, as well as potential arthropod vectors of plant diseases, are routinely introduced to the region with fresh produce for human consumption. We conclude that the risks of introducing pathogenic organisms through human activities are real and significant.

### Impacts on microbial community structure and function

Antarctic terrestrial habitats support endemic microbial taxa that have been evolutionarily isolated for extended periods [68]. In addition to endemism on a continental scale, terrestrial microbial niches in ice-free regions such as the McMurdo Dry Valleys display distinct microbial communities [69]. Clear patterns of biogeographic regionalisation are now recognised across the majority of macroscopic organism groups typical of terrestrial environments in Antarctica [70,71]. Such regional heterogeneity is interpreted as a strong signal of long-term (at least multimillion) year presence, isolation and local evolutionary radiation. Such patterns are also starting to be recognised in studies of elements of the microbial flora [72]. As a result, there is now recognition of the risks associated with anthropogenic assistance with intracontinental movement of animal and plant species indigenous to one part of the continent, as well as the genetic homogenisation that this will lead to [73]. Such risks are plainly equally pertinent to Antarctic microbial diversity, but studies are yet to specifically address this subject.

### Climate change

It is widely accepted that long-term climate change, particularly an upward temperature trend in several areas of the region [44], is likely to have a dramatic impact on Antarctic terrestrial biology [74]. It is obvious that higher mean temperatures will favour the growth of more temperate species (including invasive aliens) over those that are either slow growing or thermally sensitive. Within microbial communities, which are known to be dominated by psychrotolerant rather than obligate psychrophilic organisms, such climate changes might have a limited impact of community composition, but might be expected to increase biomass loads (e.g. by outgrowth of cryptic communities and expansion of soil crusts).

It is reasonable to assume that biological 'invasions' due to warming-induced niche modification will lead to increased biogeochemical cycling and energy flow, and increased species richness [75]. The invasion of glacier forelands by invasive plants shows that for some organisms this is already happening [46]. Such invasions may have wide ranging effects including soil stabilization, notably by cyanobacteria and mosses [76] and lower plants, and increased trophic complexity leading to higher productivity.

It is even more difficult to assess whether microbial contamination and climate change will show positive or negative synergy. With a sufficiently dramatic temperature rise, temperate (mesophilic) microbial 'aliens' might eventually outcompete indigenous microorganisms, an effect which could well be partly countered by the broadening of physiological capacity acquired by these organisms as a result of LGT.

## Concluding remarks

The anthropogenic contamination of so-called 'pristine' Antarctic environments is an extant process and can reasonably be assumed to increase with increasing human occupation of the continent. On the basis of our current knowledge of molecular, physiological and system processes, we might predict that this process will have little overt impact on extant microbial communities (unlike, e.g. the establishment of non-indigenous plant and invertebrate species on the sub-Antarctic islands). We suggest that the climatic extremes of the Antarctic continent, even in light of global warming trends, will prevent gross microbiological colonisation events (such as the invasion of New Zealand rivers by the non-indigenous diatom *Didymosphenia geminata* [77]). However, a word of warning is appropriate. The past decade has seen dramatic increases in the sensitivity and resolution of methods for studying microbial ecology. Molecular phylogenetics, whole-genome amplification and ultra-deep high-throughput sequencing (to give only three examples) have dramatically changed microbial ecology. If we assume at least a linear future trend in technological development, we must consider some future point when the microbial contamination derived from past, current and future activities could pose a serious threat to the validity of molecular ecological studies, and to the genetic integrity of Antarctic microbial ecosystems. Indeed, concerns have been growing, based on recent identifications of greater biogeographic structuring across the continent than previously appreciated, that intraregional transfers of organisms as a consequence of human activities may pose a significant conservation problem [27]. Not only would regionalism of the continent be reduced through biological homogenisation, but the ability of research to uncover historical and current patterns of endemicity might be compromised. To counter such threats might require a new tier of Antarctic Specially Protected Areas, essentially 'no-go, no-fly zones' where access would be permitted only under the strictest of conditions of biological protection, designed to provide rigorous protection of the environment from human dissemination of non-indigenous organisms. Such zones would, at the very least, provide control sites for future comparative analyses of the impacts and consequences of the anthropogenic introduction of microorganisms. They might also provide an indication of the extent to which the approaches required to understand regionalisation of the continent might, by their very nature, influence that understanding.

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