

# On the rocks: the microbiology of Antarctic Dry Valley soils

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**Abstract** | The arid soils of the Antarctic Dry Valleys constitute some of the oldest, coldest, driest and most oligotrophic soils on Earth. Early studies suggested that the Dry Valley soils contained, at best, very low levels of viable microbiota. However, recent applications of molecular methods have revealed a dramatically contrasting picture — a very wide diversity of microbial taxa, many of which are uncultured and taxonomically unique, and a community that seems to be structured solely by abiotic processes. Here we review our understanding of these extreme Antarctic terrestrial microbial communities, with particular emphasis on the factors that are involved in their development, distribution and maintenance in these cold desert environments.

## Last glacial maximum

The time of maximum extent of the ice sheets during the last glaciation approximately 20,000 years ago.

## Biota

The total collection of organisms in a geographic region.

## Trophic level

An organism's position in the food chain.

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The Antarctic continent is one of the most physically and chemically extreme terrestrial environments to be inhabited by microorganisms<sup>1</sup>. Although most of the continent is covered by glacial ice sheets, ice-free areas comprising ~0.4% of the continental land mass are discontinuously distributed around the coastal margins (BOX 1), and many of these areas seem to have been ice free since at least the last glacial maximum<sup>2</sup>. The McMurdo Dry Valleys (here after called the Dry Valleys) are a series of generally west-to-east-oriented, glacially carved valleys located between the Polar Plateau and the Ross Sea in Southern Victoria Land, Antarctica. Dry Valley soil ecosystems are characterized by large variations in temperature<sup>3–5</sup> and light regimes<sup>6</sup>, steep chemical gradients<sup>7</sup> and a high incidence of solar radiation with an elevated ultraviolet B (UVB) light component<sup>6,8,9</sup>. The microorganisms inhabiting these ice-free, cold-soil environments exist under conditions of low nutrient status<sup>10</sup> and low bioavailability of water, this being further compromised by high levels of salinity<sup>11–13</sup> (TABLE 1). The additive effects of the extreme aridity and widely fluctuating physiochemical conditions of these cold deserts are expected to have a great impact on the adaptations and life cycle strategies used by resident biota.

Soil biological research in the Dry Valleys did not have a promising beginning, as shown when Captain Robert Falcon Scott, describing his party's exploration of the Taylor Valley in 1903, wrote, "we have seen no living thing, not even a moss or lichen" (REF. 14). Descriptions of 'sterile' soil environments persisted well into the 1970s<sup>15</sup>, reflecting what we now know to be the limits of culturing techniques rather than the limits of life. Early studies that were stimulated by the search by the US National Aeronautics and

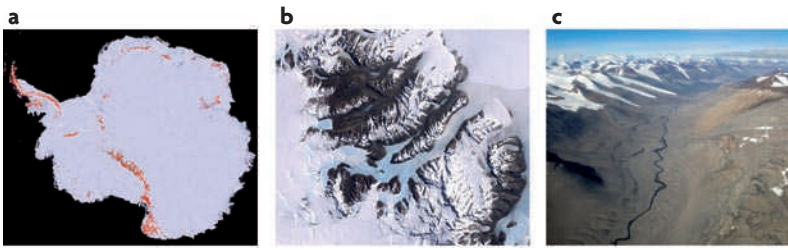
Space Administration (NASA) for analogues of lunar and Martian terrestrial 'environments' suggested that the Dry Valley mineral soils contained, at best, very low levels of viable microbiota. Today we recognize that the distribution of microbial biota is ubiquitous across the soils of the Dry Valleys, including arid mineral soils with no visually conspicuous sources of water or organic matter. The structure of these biotic communities is simple, typically being composed of only a few trophic levels and a limited number of invertebrate taxa. Recent findings suggest that, despite the severe environmental conditions and the trophic simplicity of the invertebrate communities that are present, the microbial communities are surprisingly diverse<sup>16–19</sup> and cell numbers are much higher than expected<sup>20</sup>.

This Review describes recent work in the Dry Valleys that has used molecular tools to explore the composition and structure of microbial communities that live in the soils of this harsh, arid environment. Particular attention is paid to describing those aspects of the extreme physiochemical environment that are possible driving forces behind the rich microbial diversity. This Review is timely, given the recent application of new molecular-based research to the Antarctic and the culmination of the International Polar Year (BOX 2).

## The harsh polar desert environment

The Dry Valleys are a mosaic of glaciers, ice-covered lakes, ephemeral streams and arid soils. This region is 'ice free', primarily because glacial flow from the East Antarctic Ice Sheet is obstructed by the Trans-Antarctic Mountains. Mineral soil occupies much of the ice-free area and, relative to lakes and streams, is the most 'extreme' Dry

Box 1 | The Antarctic and its main ice-free areas



At just under 13 million km<sup>2</sup>, Antarctica is the fifth largest continent on earth and only 0.4% is permanently ice-free (see the figure, part **a**; ice-free zones are highlighted in red). Large areas of exposed soil include the lower-latitude Antarctic Peninsula (of 7,763 km<sup>2</sup> in area), Eastern Antarctica, including the Vestfold Hills (10,620 km<sup>2</sup>), and the McMurdo Dry Valleys (6,861 km<sup>2</sup>). In addition, high-altitude ice-free areas include the Ellsworth and Transantarctic Mountains (14,170 km<sup>2</sup>), the North Victoria Land mountains (5,412 km<sup>2</sup> and widely distributed nanutuks (1,428 km<sup>2</sup>). The McMurdo Dry Valleys, located in Southern Victoria Land along the western coast of McMurdo Sound (between E160° and E164° longitude and S76° and S78° latitude) are the largest expanse of contiguous ice-free ground in Antarctica (see the figure, part **b**, which shows a Landsat image). The Dry Valleys are an Antarctic Specially Managed Area (ASMA) and represent over 15% of the ice-free land on the continent. Differences in geography (that is, latitude, topography and proximity to coastal margins) and geology make each of these regions widely different in terms of the factors that influence the development and maintenance of biological communities. The McMurdo Dry Valleys receive only about 6 months of light per year, with persistent strong winds, excessively low precipitation (<10 cm yr<sup>-1</sup> water equivalent) and a mean annual air temperature of near -20 °C. The valleys consist of a pristine mosaic of perennially ice-covered lakes, intermittent glacial-melt-water streams and extremely arid mineral soils surrounded by barren mountains with intersecting glaciers (see the figure, part **c**, which is of the Onyx River in the Wright Valley, Victoria Land). Even in localized geographical regions, high levels of spatial variability in physical and chemical parameters can be observed over kilometre or even metre scales<sup>5,7,99</sup>. Recent studies suggest that inter-valley and intra-valley differences in microbial community composition and structure are substantial.

Figure part **a** is courtesy of F. Morgan, Landcare, New Zealand. Figure part **b** is courtesy of the Landsat Image Mosaic of Antarctica (LIMA) Project. Figure part **c** is courtesy of R. Strachan, Antarctica New Zealand.

**Nanutuks**

Localized rocky, exposed, ice-free regions in terrestrial ice fields.

**Austral**

Of the Southern Hemisphere.

**Sublime**

Transition from the solid state to the gaseous phase with no intermediate liquid stage.

**Katabatic wind**

A wind that carries high-density air from a higher elevation down a slope under the force of gravity. In the Antarctic, the build-up of high-density, cold air over the ice sheets and the elevation of the ice sheets bring into play enormous gravitational energy, propelling the winds at well over hurricane force.

Valley ecosystem from the perspective of energy, water and nutrient constraints that are placed on the resident biological communities. Dry Valley soils originate from weathering of bedrock and glacial tills that consist of granites, sandstones, basalts and metamorphic rocks.

Air and soil temperatures are highly variable in the Dry Valleys. Depending on aspect, altitude and other topographical factors, mean annual temperatures range from -15 °C to -30 °C<sup>4</sup>. However, surface soils are subject to large daily temperature fluctuations during the austral summer periods, with 25–75 days when temperatures exceed 0 °C and liquid water is potentially available<sup>4,21</sup>. Maximum temperatures in the range of 17–26 °C are typical, and daily temperature fluctuations of >20 °C are not unusual, often resulting in multiple freeze–thaw cycles in a single day<sup>5,22</sup>. In the winter months, minimum temperatures typically range from -40 to -60 °C.

Dry Valley surface mineral soils are extremely dry, with typically <2% mass water content, which is equivalent to the water content in many of the world's hottest deserts. Precipitation is very low, generally <10 cm yr<sup>-1</sup> water equivalent<sup>23</sup>, and always in the form of snow, much of which sublimates before reaching soils<sup>24</sup>. In addition, rapid evaporation is driven by the very low relative humidity of the

katabatic winds that descend from the polar plateau into the open valleys<sup>25</sup>. However, unlike in hot deserts, large reservoirs of water are closely associated with Dry Valley surface soils; half of the soils in the Dry Valleys have subsurface ice, either as buried massive ice or as ice-cemented soil<sup>26</sup>. The permafrost layer is typically within 30 cm of the soil surface<sup>26</sup>. A wetted zone often occurs between this permafrost level and the overriding active soil layer, and biota and organic matter are most prevalent in this zone; in the Taylor Valley, this typically occurs at depths of between 5 cm and 10 cm from the soil surface<sup>62</sup>. The large humidity gradient between shallow wet soils and dry surface air is thought to drive substantial transport of water from the subsurface<sup>27</sup>. Liquid water can persist on mineral surfaces at very low temperatures<sup>28</sup>, and it is assumed that either biological activity in the soils occurs in these thin water films, or that some microorganisms have the capacity to absorb water vapour directly. In warm summers, enhanced melting of subsurface ice contributes to higher levels of soil water availability and greater biological activity<sup>21</sup>.

Although temperature and water availability are thought to crucially influence the composition and survival of biological communities, other factors may also be important. These include radiation (UVA and UVB radiation and photosynthetically active radiation (PAR)), the physical stability of soil surfaces and the geochemical properties of local soil. For example, the extreme age of Antarctic soils, which have a history of continued aerosol deposition and very low leaching rates, has resulted in large salt imbalances compared with the salt levels of temperate soils<sup>12</sup>. The resulting geochemical gradients may impose strong limitations on the distribution of soil biota<sup>7,29</sup>.

The composition of Dry Valley communities and the survival strategies of resident organisms are consequences of the harsh Antarctic conditions. No vascular plants or vertebrates inhabit the Dry Valleys, and soil food webs are composed almost entirely of microorganisms, with few metazoan invertebrate taxa<sup>30</sup> (BOX 3). Although recent work has suggested that there is a much greater microbial diversity than previously recognized<sup>17,18,20</sup>, the diversity in invertebrate taxa is extremely low, with nematodes often being the sole metazoan taxon<sup>31</sup>. The simplicity of these food webs makes Antarctic ecosystems useful model systems for investigating relationships between biodiversity and ecosystem function.

Multiple sources of organic matter are thought to contribute to Dry Valley soil carbon pools and food webs. Algae, cyanobacteria, lichens and mosses are present in some soils and lithic environments<sup>32</sup>, but reported rates of carbon fixation are extremely low (for example, 1–20 g carbon m<sup>-2</sup> yr<sup>-1</sup>)<sup>33,34</sup>. Owing to this low productivity and to the climatic limitations on decomposition, carbon accumulation and turnover in the Dry Valleys is thought to operate over long timescales, perhaps centuries to millennia<sup>35</sup>. For example, some organic matter in Taylor Valley soils have carbon and nitrogen isotopic signatures that resemble lacustrine sediments, but these samples are at elevations well above current lake levels<sup>36</sup>. These findings suggest that soil organic-matter stocks are influenced

Table 1 | Properties of the McMurdo Dry Valleys and other desert environments

Site	Latitude	Mean annual temperature (°C)	Mean summer temperature (°C)	Mean annual precipitation (cm water equivalent)	Soil organic carbon (g kg <sup>-1</sup> )	Microbial biomass (g kg <sup>-1</sup> )
Beacon Valley, Antarctica*	S78 °	-23	-5	Not available	0.02–0.40	0 <sup>†</sup> –0.047
Taylor Valley, Antarctica <sup>21</sup>	S77 °	-18	0.2	<10	0.16–0.63	0.003–0.043
Garwood Valley, Antarctica <sup>37,108</sup>	S78 °	-10	3.8	Not available	0.27–3.04	0.003–0.042
Sonoran Desert, Arizona, US <sup>109</sup>	N33 °	23	37	21	5–25	0.025–0.125
High Arctic Desert, north eastern Greenland <sup>110</sup>	N74 °	-10	3.5	20	51–56	0.416–0.648

\*Met station observations for January 2003 to January 2005 (J.E.B., unpublished observations). <sup>†</sup>The lower range for microbial biomass for the Beacon Valley is below detection limits.

#### Permafrost layer

Soil that is at or below the freezing point of water (0 °C or 32 °F) for ≥2 years.

#### Lithic environment

An environment that relates to or is composed of stone.

#### Lacustrine sediments

Lake sediments

#### Aeolian redistribution

Wind dispersal

#### Ornithogenic

Derived from the deposition of the faecal matter of various bird species; ornithogenic material is a major source of nutrient input in the maritime Antarctic.

#### Fell-field soil

Soil in an environment, usually alpine or tundra, where the dynamics of frost (freeze and thaw cycles) and of wind give rise to characteristic plant forms in scree interstices. In addition, the high porosity of the soil makes a fell-field a difficult place for plants to grow.

#### Psychrophilic

Pertaining to an organism that prefers cold temperatures.

#### Hypolithic

Pertaining to an organism that lives underneath rocks in climatically extreme deserts.

by a legacy of lacustrine sediments that were deposited during high lake stands at the last glacial maximum. In other valleys, contemporary inputs of carbon may come from aeolian redistribution of the cyanobacterial mats that occupy lake margins<sup>37,38</sup>. Similarly, marine inputs of organic matter in coastal regions or under mummified seal carcasses provide localized sources of exogenous organic matter that support distinct microbial and invertebrate communities<sup>17</sup>. It remains unclear to what extent soil food webs rely on exogenous sources of organic matter or on carbon fixed *in situ*. Understanding the biological and physical influences on the accumulation and turnover of carbon is crucial to understanding how the assembly and activity of soil communities in the Dry Valley region are controlled<sup>39</sup>.

### Microbial diversity in Dry Valley soils

Prior to the molecular age of microbial ecology, Dry Valley microbiology was studied solely by cultivation and microscopy. Many early studies suggested that either soils from the Dry Valleys were sterile<sup>1,15,40–44</sup>, or the soil bacterial diversity and abundance was extremely low<sup>3,10,33,45–47</sup>. This is in stark contrast to nutrient-rich and water-rich ornithogenic soils and fell-field soils of coastal Antarctica and the sub-Antarctic, which, like lake sediments, support vastly higher microbial counts<sup>47–49</sup>. It is now well recognized that, for most natural systems, culture-based studies underrepresent the abundance and diversity of bacteria that are fastidious, co-culture-dependent or in a viable but non-culturable state<sup>50–52</sup>. Furthermore, the results of many early pioneering isolation studies were biased in their outcomes owing to the choice of culture media, a limitation that was recognized at the time. These culture-based studies suggested that the microbiology of Antarctic mineral soils was dominated by a small number of aerobic cosmopolitan groups with only a few anaerobic isolates<sup>33,45</sup>. The largest study of bacterial isolates (which encompassed 130 samples) from the Dry Valleys revealed that Actinobacteria such as *Arthrobacter* spp.,

*Brevibacterium* spp. and *Corynebacterium* spp. were prominent<sup>53</sup>. Other members of the Actinobacteria were also present, including representatives of the genera *Micrococcus*, *Nocardia* and *Streptomyces* along with *Bacillus* spp., *Flavobacterium* spp. and *Acinetobacter* spp. isolates.

Recent molecular-based phylogenetic studies of Dry Valley microbial populations<sup>16,19,54,55</sup> have provided some indication of the true diversity of microorganisms in these soil communities (FIG. 1), finding it to be surprisingly high<sup>16</sup>. This was unexpected, considering the extreme nature and trophic simplicity of these systems. In general, a substantial percentage of the community is unknown at the class level. However, many of the identifiable microbial taxa affiliate with known isolates that resist desiccation, are halotolerant and are often psychrophilic or psychrotolerant. Archaeal phylotypes have only recently been detected in Dry Valley soils and hypolithic samples<sup>56</sup>.

Bacterial communities in the Dry Valleys contain representatives of at least 14 different phyla of bacteria (FIG. 1), with the most dominant being from the Acidobacteria, Actinobacteria and Bacteroidetes. Conversely, the Proteobacteria phylum is generally poorly represented in Dry Valley soils<sup>16,19,55</sup>. Comparisons with clone libraries from other Antarctic soils, mainly on the Antarctic Peninsula, indicate that in these environments members of the Proteobacteria are in fact the most dominant members of the community<sup>18</sup> (FIG. 1). It should be stressed that the Antarctic Peninsula is very different, both biologically and environmentally, to the Dry Valleys, being much warmer and wetter, with a greater maritime influence and frequent plant colonization. However, in this comparison the sites chosen were those that are most comparable to the Dry Valleys (being fell-field soils with low water content in the Antarctic Circle). Likewise, a comprehensive survey of clone libraries from 21 surface soils from temperate zones<sup>57</sup> (FIG. 1) found the dominant phyla were the Proteobacteria and Acidobacteria. The

## Box 2 | The International Polar Year

The International Polar Year (IPY) 2007–2009 was a major international effort seeking to galvanize global research in polar regions, sponsored by the International Council for Science and the World Meteorological Organization. Following in the historical footsteps of 3 previous IPYs (1882–1883, 1932–1933 and 1957–1958), the recent IPY included over 60 participating nations and sponsored over 200 integrated projects involving thousands of scientists working in both Arctic and Antarctic systems. Projects included a wide range of biological, physical and social research topics, including major efforts to understand the role of bacteria in these harsh systems. The IPY enabled many of the participating countries to make their first forays into polar research by sharing costs with those countries that have historically invested in the necessary infrastructure, to maximize capability and research output. Mounting evidence of changes in the duration and area of snow cover, of substantial glacier retreat and of reductions in the thickness and extent of sea ice in polar regions, owing to a warming climate, intensified the importance of the recent IPY. As a direct result of the IPY, numerous programmes (such as Microbiological and Ecological Responses to Global Environmental Changes in Polar Regions, Census of Antarctic Marine Life, Evolution and Biodiversity in Antarctica, and Polar Aquatic Microbial Ecology) have been initiated to continue these newly established international collaborations.

*Deinococcus–Thermus* and Gemmatimonadetes clades, which have low or no representation in other surface soils, are relatively common in Dry Valley clone libraries. Together, these data suggest that microbial community composition in Dry Valley soils is fundamentally different from that in temperate soils. A comparison of the bacterial diversities of Dry Valley soils and a dry hot desert soil (from the Tataouine Desert of Tunisia) also shows striking differences. In the Tataouine Desert, bacterial diversity seems to be much lower and completely dominated by gammaproteobacteria, Actinobacteria and, to a lesser extent, Acidobacteria<sup>58</sup>.

## Community dynamics

Although the increasing catalogue of phylogenetic surveys of microbial diversity in Antarctic desert soils<sup>5,16,19,59,60</sup> suggests that complex and heterogeneous populations of prokaryotic and eukaryotic microorganisms exist, fundamental questions remain about the structure and function of these communities. For example, are the organisms in these soils sufficiently active to contribute to biogeochemical cycling or ecological processes? Where do they originate from, and do they constitute a genuine community, supporting biotic interactions (such as feeding and competition) in and across trophic levels? Are these communities stable, and how do community functions respond to variable or changing environmental conditions?

The extreme nature of the Dry Valley soil environment would be expected to limit microbial colonization, activity and interactions; however, at least some of the microorganisms in Antarctic desert soils are metabolically active. Radiolabelling<sup>61</sup> and CO<sub>2</sub> efflux<sup>62–64</sup> studies

have consistently shown that bulk metabolic processes (such as respiration) are detectable and responsive to environmental variables<sup>22</sup>. Furthermore, supplementing soils with exogenous substrates<sup>64</sup> triggers responses in microbial populations due to the increased availability of nutrients. Microbial respiration rates quantified by CO<sub>2</sub> efflux measurements were  $0.1 \pm 0.08 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ , which is two orders of magnitude higher than those measured for cryptoendolithic communities<sup>65</sup> and an order of magnitude lower than values for Antarctic streams<sup>66</sup>. By comparison, average soil respiration rates reported for warm desert soils and Arctic tundra are approximately  $0.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$  and  $1.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ , respectively<sup>67</sup>.

There is also a growing consensus that these ‘assemblages’ do constitute microbial communities with a functional, if simple, trophic structure. At its simplest level, such a community might be exclusively microbial and consist of primary producers (photoautotrophic cyanobacteria) and degraders (heterotrophic bacteria and fungi). The contention that both of these capacities exist in Antarctic desert soils is supported by several recent lines of evidence. First, the capacity for both carbon and nitrogen fixation exists in bulk desert soils; phylogenetic surveys have repeatedly identified members of the phylum Cyanobacteria (such as *Nostoc* spp., *Oscillatoria* spp., *Leptolyngbya* spp., *Phormidium* spp. and *Synechococcus* spp.<sup>16,68,69</sup>), not all of which are phylotypes that are typically derived from aeolian distribution of lacustrine biomass (*Leptolyngbya* spp., for example, are not)<sup>69</sup>. Stable isotope analysis shows that these soils have depleted <sup>13</sup>C signals that are typical of autotrophic fixation<sup>36,38</sup>. We conclude that the photoautotrophic capacity of the cyanobacterial populations in Dry Valley soils is at least hypothetically capable of supporting a functional community. However, no empirical data on autotrophic carbon or nitrogen fixation rates or even indicators of putative fixation rates (such as data about the expression levels of Rubisco and the nitrogenase *Nif* genes) have been reported to date. This suggests the need for high-sensitivity, quantitative analyses to establish the carbon and nitrogen input rates in such extreme systems. We have recently shown that Dry Valley hypolithic communities have measurable N<sub>2</sub>-fixation rates (as determined by acetylene reduction) (D. Capone, D.A.C. and J. Sohm, unpublished observations). The proposal that microbial communities in Antarctic desert soils are capable of autotrophic processes does not preclude a parallel dependence on heterotrophic substrates. It has been proposed and indirectly supported by phylogenetic surveys that exogenous lacustrine biomass is an important source of carbon and nitrogen in Dry Valley soils<sup>36,64,69</sup>.

Further support of the contention that functional trophic structures exist in Dry Valley soils is provided by the presence of populations of heterotrophic microorganisms<sup>70</sup>. Catalogues of Antarctic soil isolates (summarized in REF. 71) almost exclusively comprise heterotrophic taxa, and phylotypic surveys show a high proportion of phylotypes such as the Actinobacteria, which are likely to possess heterotrophic physiologies.

## Cryptoendolithic

Pertaining to an organism that colonizes structural cavities within porous rock.

## Photoautotrophic

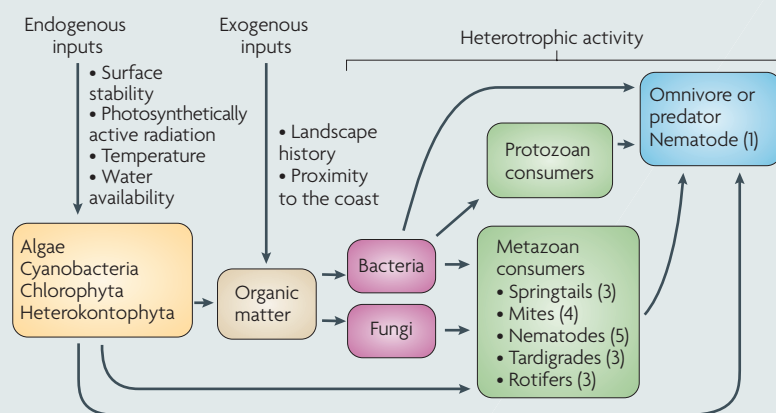
Pertaining to an organism that is capable of synthesizing its own food using light.

## Heterotrophic

Pertaining to an organism that is capable of synthesizing its own food using chemical energy from inorganic substances.



### Box 3 | Controls over biodiversity in the harsh Antarctic environment



The harsh Antarctic environment marks the limit of multitrophic communities in terrestrial ecosystems. Many of the McMurdo Dry Valley soils lack metazoan species altogether, and even the most suitable habitats support food webs consisting of low numbers of invertebrates<sup>31</sup>. As a function of their low diversity, invertebrate communities are well described compared with microbial communities (consisting of bacteria, fungi and protozoans), the diversity of which remains undersampled; most of the extant information about these microbial communities has been gleaned from culture-based studies. The metazoan fauna of this region is limited to <5 genera per phylum (see the figure, in which the number in parentheses is the number of genera per phylum), with a high incidence of endemism<sup>30</sup>. Communities consisting of >3 trophic levels are rare<sup>99</sup>. These depauperate communities result in an absence of major feeding groups, and most of the soil environments lack higher consumers or predators. The trophic simplicity of Antarctic soil ecosystems is a consequence of the physiological challenges that are imposed by both the extreme climate and the soil biogeochemical properties<sup>100</sup>. The paucity of liquid water, which is a result of frigid temperatures and low precipitation, is a key limitation to the development of a soil biota<sup>101</sup>. Owing to this aridity, the accumulation of salts in evaporative zones or on ancient surfaces also limits the distribution of soil biota<sup>7,102</sup>. The climate also constrains the activities of photoautotrophs (that is, cyanobacteria, algae, lichens and mosses), which limits the energy available to support complex food webs<sup>21</sup>. Sources of soil organic matter include both endogenous inputs from photoautotrophs and exogenous inputs related to landscape history (for example, lake inundation and sediment deposition) and marine inputs (such as penguins or seals). Therefore, the distribution and activity of soil organisms are closely linked to spatial patterns of soil biogeochemistry. Microbial diversity and abundance are probably influenced by similar abiotic drivers.

#### Mesic soil

Soil with a moderate or well-balanced supply of moisture.

#### Psychrotrophic

Pertaining to an organism that is capable of surviving or even thriving in a cold environment.

#### Mesophilic

Pertaining to an organism that grows best in moderate temperatures, typically between 15 °C and 40 °C (77 °F and 104 °F).

#### Chasmolithic

Pertaining to an organism that colonizes fissures and cracks in the rock.

The involvement of higher trophic levels in Antarctic soil microbial communities is less clear. Protists and one species of endemic microbial-feeding nematode (*Scottinema lindsayae*) are present in the majority of dry soils of the region<sup>30,31</sup> and are evidently limited only by the high salinity of old soil surfaces<sup>7,29</sup>. By contrast, multitaxa communities of other eukaryotic consumers, including rotifers, tardigrades, mites and springtails, are restricted to more mesic soil environments adjacent to streams, lakes and ponds<sup>30,72,73</sup>. These observations indicate that Dry Valley soils constitute one of the simplest trophic structures in the terrestrial biosphere, consisting essentially of a two-tier microbial–metazoan system (BOX 3). Interestingly, even in moist soil habitats no clear relationship is evident between the presence and diversity of metazoan consumer trophic levels and microbial diversity<sup>17</sup>, suggesting that top-down controls of consumers on lower trophic levels may be limited in these extreme conditions.

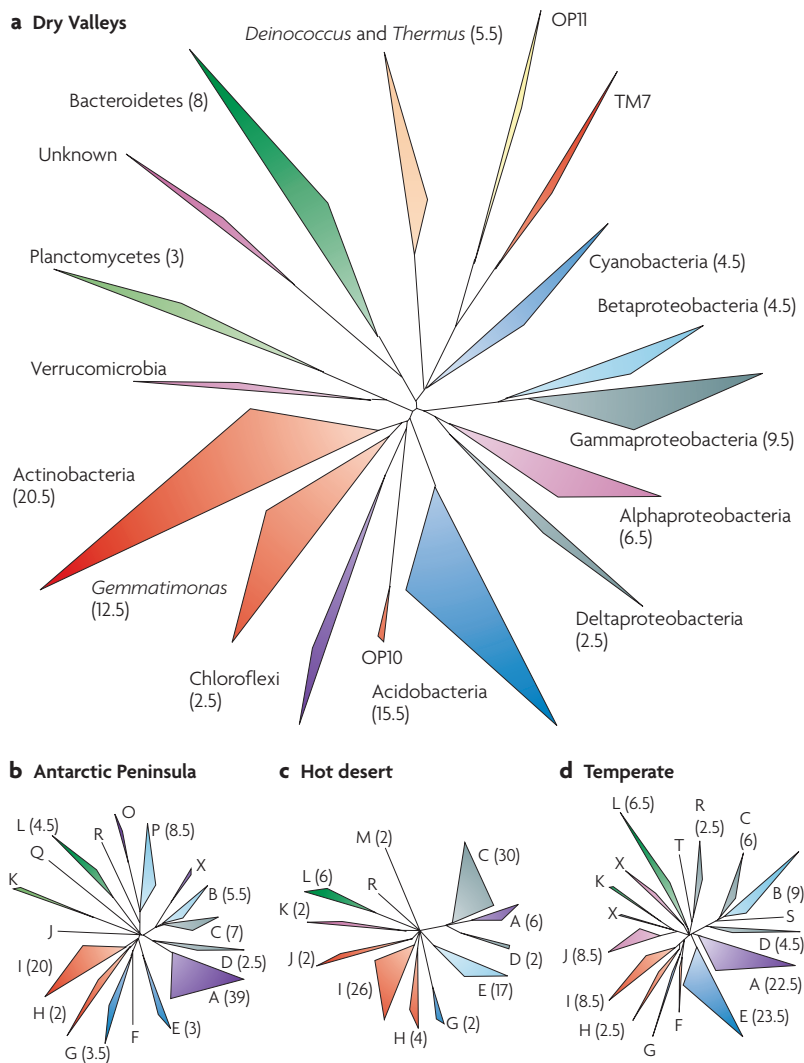
Sources of microbial diversity in Dry Valley soils remain largely unresolved. Theoretically, extant microorganisms may have evolved *in situ*, may be sourced locally (for example, on windborne particles) or may be sourced from considerable distances through the movement of fine particles in high-altitude jet stream airflows<sup>74,75</sup>. Phylogenetic surveys show phylotypic affinities with local (marine and lacustrine) sources, non-Antarctic affiliations and a high proportion of sequences with no identifiable regional affinity. The presence of a high proportion of indigenous taxa is evident from the psychrotrophic or (less commonly) psychrophilic growth characteristics of Antarctic soil isolates<sup>76</sup>. A number of genera unique to the Antarctic (for example, *Psychrobacter*) have been catalogued. Conversely, microbial strains with mesophilic cardinal growth temperatures can also be readily isolated from Antarctic soils. It is now becoming clear that bacterial community structure in different locations (that is, valleys or coastal and inland sites) are distinct, suggesting they are being influenced by either contemporary or historical local environmental conditions<sup>17</sup>.

Little is known about the quantitative impacts of the environmental extremes that are typical of the Antarctic Dry Valleys. However, the presence of macroscopic communities in only protected environments (largely chasmolithic<sup>68</sup>, hypolithic<sup>77</sup> and endolithic<sup>78</sup> environments) strongly suggests that surface impacts are sufficiently severe to limit macroscopic community development. We suggest that the key drivers for community development are light (to support autotrophic processes and effect UV damage), water (to support biological processes) and, in some places, physical stability. Surface mineral soils (at a depth of 0–5 mm) receive high incident PAR during the short Antarctic summer periods<sup>6</sup> but they can be mobile. Desert pavements, however, are typically quite stable. Subsurface soils are highly physically stable, receive little or no incident light and maintain a higher relative humidity than surface mineral soils or desert pavements due to the underlying permafrost. Chasmolithic, hypolithic and endolithic habitats contribute positively to the key requirements, providing physical stability, PAR transmission up to a few centimetres depth and, for hypoliths, the possibility of condensation surfaces for the capture of subsurface water vapour.

The flux of UVA and UVB is currently substantially higher on the Antarctic continent than elsewhere in the world as a result of the polar ozone hole depletion and longer day lengths during the austral summer<sup>79</sup>. It has been proposed that UV impact is an important factor in controlling surface microbial community development<sup>9</sup>. For example, some Antarctic organisms are known to accumulate UV-protective compounds such as scytonemin, carotenoids, anthraquinones and mycosporine-like amino acids<sup>80</sup>.

#### Microniches in Antarctic desert systems

The Dry Valleys are by no means homogeneous ecosystems. Apart from the aquatic ecosystems (glacial streams, lakes and saline ponds), the severity of the Dry Valley environment and extreme desiccation has led to the development of microbial communities in protected



**Figure 1 | Phylogenetic diversity of bacterial 16S ribosomal RNA gene sequences from the McMurdo Dry Valleys, Antarctica, and comparison with bacterial diversity in clone libraries from the Antarctic Peninsula, a hot desert and temperate surface soils.** The trees were constructed using ARB<sup>103</sup>, with DNADIST and Neighbour Joining analysis. This shows the high diversity seen within different bacterial phyla and also the percentage of sequences (shown in brackets). OP10, OP11, TM7 and WS3 are candidate divisions that represent bacteria that have not yet been isolated and cultured. **a** | A total of 426 sequences were included in the analysis of McMurdo Dry Valley diversity, from studies in the Miers Valley<sup>16</sup> (S.C.C. and I.R.M., unpublished observations), Luther Vale<sup>19</sup>, and Bull Pass and Vanda in the Wright Valley<sup>5</sup>. **b** | Antarctic Peninsula sequences (328 in total) are from studies of Mars Oasis, Fossil Bluff, Coal Nunatak and Anchorage Island; these are fell-field sites in the Antarctic Circle and were selected as the most similar environments to the Dry Valleys from this much larger study<sup>18</sup>. **c** | Hot desert sequences (116 in total) are from a study of the Tataouine Desert in Tunisia<sup>58</sup>. **d** | Temperate surface soil sequences (426 in total) are from studies in the United States and United Kingdom<sup>104–107</sup>. A, alphaproteobacteria; B, betaproteobacteria; C, gammaproteobacteria; D, deltaproteobacteria; E, Acidobacteria; F, OP10; G, Chloroflexi; H, *Gemmatimonas*; I, Actinobacteria; J, Verrucomicrobia; K, Planctomycetes; L, Bacteroidetes; M, *Deinococcus* and *Thermus*; O, TM7; P, cyanobacteria; Q, Fusobacteria; R, Firmicutes; S, epsilonproteobacteria; T, WS3; X, unknown isolates.

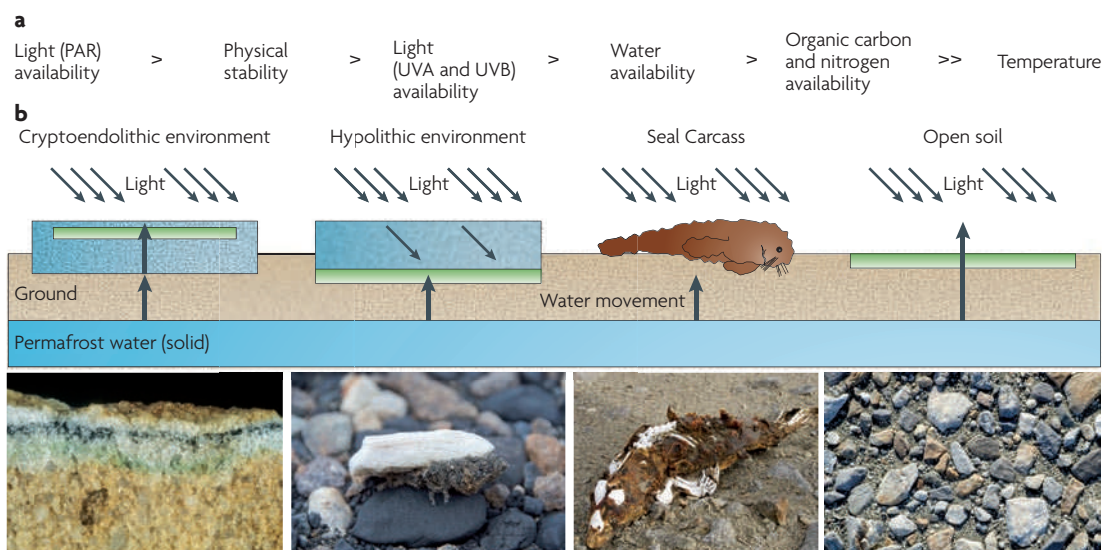
environments (known as refugia)<sup>81</sup> (FIG. 2; TABLE 2). The most substantial of these are the lithic environments, where well-developed microbial communities have colonized cracks in rocks, the undersides of translucent rocks and the subsurface interstices of coarse crystalline rock types.

The best characterized microniche communities are the cryptoendolithic microbial consortia. These communities are typically found in the fine-grained Beacon sandstones, which are the dominant substrata of the northern Dry Valleys, but they also occur in coarse-grained quartzites and limestones<sup>68</sup>. These mineral types offer a combination of porosity (providing interstitial spaces for microbial colonization) and translucence (facilitating photosynthetic activity), which together permit zonal growth a few millimetres below the rock surface (FIG. 2). Cryptoendolithic microbial populations are protected from physical abrasion by wind-blown sand and buffered from rapid thermal fluctuations<sup>47</sup> despite being in equilibrium with the external temperature for much of the Antarctic year (TABLE 2). Cryptoendolithic environments contain an extensive and varied microbial community, some of which are dominated by the cyanobacteria, alphaproteobacteria and *Deinococcus* spp., whereas others are known to be composed primarily of eukaryotic algae, fungi and lichens<sup>54,65,82,83</sup>.

Hypolithic communities exist on the undersides and around the margins of translucent rocks (such as quartz and marble) of Dry Valley desert pavement (FIG. 2). The overlying translucent rock permits light transmission to a depth where photoautotrophs, such as moss and cyanobacteria, can survive, which may facilitate the development of more complex heterotrophic microbial communities. Potentially beneficial elements of the hypolithic microenvironment include physical stability, desiccation buffering, increased water availability and protection from UV fluxes (TABLE 2). Although it is suggested that hot-desert hypoliths provide a greenhouse effect, protecting the sublithic organisms from extremes of temperature<sup>84</sup>, hypoliths in the Antarctic desert seem to provide little or no temperature buffering, but they do provide a significantly increased local humidity (S.C.C., D.A.C. and N. Khan, unpublished observations). Hypolithic communities also represent local 'hotspots' of microbial diversity<sup>77</sup> and productivity. Average productivity values for these communities ( $0.8 \pm 0.3$  g fixed carbon  $\text{m}^{-2} \text{y}^{-1}$ ) are equivalent to those of macroscopic lichens and bryophytes<sup>81</sup> and are possibly orders of magnitude higher than productivity levels in open Dry Valley soils.

Chasmolithic communities are common in the Dry Valleys, particularly in zones of granite, where laminar weathering produces surface rock 'flakes', under which the communities develop. These communities are typically lichen based and are evident from the extrusion of the lichen fruiting bodies around the margins of the flakes (FIG. 2). To date, no detailed molecular phylogenetic studies of these communities have been undertaken.

Another unique microniche that exists in the Dry Valleys is associated with mummified seal carcasses (FIG. 2). Hundreds of mummified crabeater seal (*Lobodon carcinophaga*) and Weddell seal (*Leptonychotes weddelli*) carcasses are found patchily distributed across many of the Dry Valleys<sup>85</sup>. These are often in very remote areas at considerable distances (from tens to hundreds of kilometres) from either the sea or the nearest seal colonies. Captain Scott first described these enigmatic oddities during his Antarctic expedition of 1901–1904,



**Figure 2 | Schematic comparisons of unique Antarctic desert soil habitats. a** | The proposed relative importance of physicochemical factors in the development of stable lithic microbial communities in Antarctic desert soils. **b** | Left to right: a cryptoendolithic community in a fractured fine-grained marble, an overturned quartz rock showing the underlying moss-dominated hypolithic community, a mummified seal carcass and a Dry Valley surface soil pavement. Part **b** image of the cryptoendolithic community courtesy of E. Friedmann, Florida State University, Tallahassee, Florida, USA.

when he observed a mummified seal in the Taylor Valley and wrote: “How it came to be there is beyond guessing. It certainly is a valley of the dead” (REF. 14). The apparent radiocarbon dates of these carcasses have ranged from 615 to 4,500 years<sup>86,87</sup>, but these dates must be taken with caution owing to the anomalies associated with dating Antarctic marine life<sup>88</sup>. Carbon that supports the growth of marine life in the Southern Ocean originates from the upwelling of ancient deep water that produces a <sup>14</sup>C activity that is much lower than the world standard for atmospheric CO<sub>2</sub>.

However, in direct analogy to deep marine whale falls<sup>89</sup>, the mummified seal carcasses in the Antarctic Dry Valleys are a natural phenomenon that provides a unique opportunity to study the effects of a localized, long-term, continuous exogenous nutrient input on the active bacterial community in an environment that is otherwise deprived of energy (that is, carbon and nitrogen). Similarly to the hypolithic system described above, but on a larger scale, the seal carcasses influence the soil beneath them by stabilizing the physical environment and reducing the immediate dehydrating effects of wind. As a consequence, moisture originating from the underlying permafrost migrates farther towards the surface and accumulates in the soil directly under the seal, fostering a unique environment for microbial growth (TABLE 2). In a recent molecular phylogenetic study, the bacterial community that was sampled from beneath the mummified seal was dominated by a diverse community of Actinobacteria, Firmicutes, gammaproteobacteria and Bacteroidetes, none of which appeared in any of the samples taken from areas without a mummified seal carcass (S.C.C. and I.R.M., unpublished observations).

#### Endolithic

Pertaining to an organism (archaeum, bacterium, fungus, lichen, alga or amoeba) that lives inside rock, coral or animal shells or in the pores between the mineral grains of a rock.

#### Sensitivity to Climate Change

The McMurdo Dry Valley region has experienced periods of warming and cooling in recent decades<sup>4,90–92</sup>, as well as discrete seasonal warming events during the 1986–1987, 1990–1991, 2001–2002 and 2008–2010 summers, resulting in an enhanced melting of glaciers and permafrost that contributed to record stream flow and lake level increases<sup>93</sup>. Both climate warming and cooling have contributed to substantial changes in the structure and functioning of the aquatic and terrestrial ecosystems that comprise the Dry Valleys<sup>4,22,21,94,95</sup>. Soils, in particular, are sensitive to climate change and variability. A cooling trend of 0.07 °C per year between 1986 and 2001 was associated with a 60% decline in the dominant invertebrate species<sup>4,22</sup>, and a summer warming and melting event in January 2002 stimulated soil diversity and microbial biomass<sup>21</sup>. Robust climate forecasts for the Dry Valleys are not possible, given the paucity of available data and our limited understanding of the current drivers influencing surface temperatures in Eastern Antarctica<sup>92</sup>. The potential effects of climate change on soil microbial communities are even more uncertain, but it is possible that any notable warming would be accompanied by longer growing seasons, which, together with higher overall temperatures, would heighten microbial activity and biogeochemical cycling. Warmer temperatures could also contribute to substantial shifts in community composition and biodiversity, reflecting changes in the dominance of cold-adapted species over more generalist species. For example, the combined influences of future climate change and the introduction of non-native microbial species through increased human activities on the continent<sup>96</sup> could result in changes in the structure of microbial communities. This is especially relevant given the observations that species interactions that can buffer responses to change in other ecosystems,



**Abiotic**  
Not associated with or derived  
from living organisms.

Table 2 | **Key environmental parameters of the main Antarctic desert habitats**

Environmental parameter	Cryptoendolithic environment	Hypolithic environment	Seal carcass	Open soil
Water source	Snow and soil humidity	Soil humidity	Soil humidity	Snow and soil humidity
Response of habitat to temperature change	Very responsive	Moderately responsive	Poorly responsive	Very responsive
Principal carbon source	Photoautotrophy	Photoautotrophy	Exogenous source	Aeolian and lacustrine sources
Principal nitrogen source	Atmospheric deposition	Nitrogen fixation	Exogenous source	Atmospheric deposition
Aeolian impact on physical stability	Negligible	Very low	Low	Very high
Light (PAR) availability	Low	Low	Very low	High
Light (UV types A and B) impact	Low	Very low	Negligible	High
Dominant bacterial phylotypes	Cyanobacteria	Cyanobacteria	Gammaproteobacteria and Actinobacteria	Actinobacteria

PAR, photosynthetically active radiation; UV, ultraviolet.

such as competition and top-down controls on microbial competition, have not been observed in these Antarctic systems<sup>97</sup>. However, as microbial communities and the potential trophic interactions of Dry Valley food webs remain poorly understood, predictions about the influences of future environmental changes on these ecosystems remain entirely speculative.

## Concluding remarks

Recent studies in the Dry Valleys, which have questioned the long-held view that there is little or no microbial life in these mineral soils, have now shown that considerable and varied microbial diversity seems to thrive in this very cold, dry and nutrient-poor environment. It is also becoming clearer from several recent inter-valley comparative studies that abiotic factors could potentially be the primary driving forces behind this diversity and that interactions between different trophic levels may play only a small part.

One of the crucial remaining issues is to identify which microorganisms are active and what factors are driving their activity. An inherent problem of using DNA markers as a proxy for diversity is that this only tells us which bacteria are present or, more precisely, what DNA has persisted in the ideal preservation condition of a dry, cold, salty environment. To this end, researchers have begun to

examine the metabolic activity of Dry Valley soil microbial communities using classical approaches, including monitoring respiration and thymidine or leucine uptake and carrying out stable-isotope probing. New RNA extraction and quantitative gene amplification protocols are now being applied, enabling researchers to successfully obtain and assess the expression of key diagnostic gene transcripts from these communities that have been manipulated in either the field or the laboratory. Recently, advanced microarray technologies have been applied to interrogate DNA extracted from similar soils to resolve both community composition and function<sup>98</sup>. These sensitive technologies could also be applied to examine RNA extracted from Dry Valley soils to determine the composition and metabolic status of the more active components of the community. In the near future, metagenomic studies linked with expression profiling will provide the necessary resolution to not only define the active component of these communities but also provide a rich resource of information on how these bacteria survive under such extreme conditions. The metagenomic data will also provide crucial information on the functional capabilities of the resident microflora, which will aid in developing new isolation strategies to access currently unculturable diversity, ultimately leading to a better understanding of the evolution and endemic nature of these isolated communities.

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## Competing interests statement

The authors declare no competing financial interests.

## FURTHER INFORMATION

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