

## Chapter 2

# Bacterial Community Structures of Antarctic Soils

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**Abstract** Antarctica's ice-free environments span diverse habitats, ranging from well developed and nutrient rich soils in the coastal areas, to poorly developed and oligotrophic soils in the continent's deserts and high elevation sites. Though most terrestrial environments in Antarctica are typified by harsh environmental conditions, many soils are home to abundant and diverse bacterial communities. These communities are locally adapted, varying both between and within different regions of the continent, and typically reflecting the local physicochemical and biological characteristics of the soils. Environmental conditions are changing rapidly in many areas, due to increased human activity on the continent and the impacts of climate change. This chapter reviews characteristics of bacterial communities in soils across Antarctica in relation to their environment, and discusses the potential responses of bacterial communities to contemporary environmental change. Continued and coordinated efforts to understand bacterial community structure and function in Antarctic soils will be necessary to monitor and predict ecological responses in these changing environments, and to shape management practices that will ensure the protection and preservation of biodiversity in Antarctica's terrestrial ecosystems.

## 2.1 Introduction

While the majority of continental Antarctica is permanently covered by the Antarctic Ice Sheet, approximately 0.35 % of the continent remains free from ice and snow cover for part or all of the year (Hopkins et al. 2006b). These ice-free areas are largely confined to the perimeter of the continent at coastal sites and regions cut off

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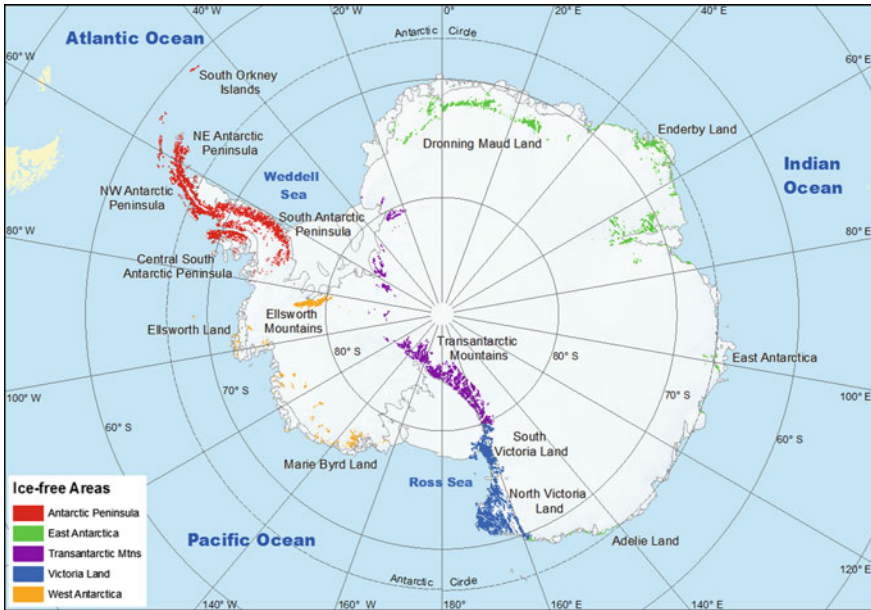
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from the Antarctic Ice Sheet, but also include isolated nunataks and mountain peaks that protrude through the extensive ice cover of the Antarctic Plateau. Soils exist in these ice-free regions at various stages of development (Vincent 1988), varying greatly in age and physicochemistry and influenced uniquely by local climate, geography, and biology (Claridge and Campbell 1985). Though exposed soils make up only a small proportion of the continent, they are important terrestrial oases that support unique edaphic (soil associated) communities.

The harsh environmental conditions of continental Antarctica have shaped soil ecosystems of low diversity and simple trophic structure. In most areas of the continent, soil organisms face severe conditions, including low water and nutrient availability, extremely cold temperatures, frequent freeze–thaw cycles, periods of prolonged darkness in winter, and exposure to high levels of ultraviolet radiation in summer (Cary et al. 2010). Conditions across most of the continent are inhospitable to many plant and animal populations that are common in temperate soils. With the exception of the Antarctic Peninsula and surrounding subantarctic islands, vascular plants are absent from Antarctic soils, with vegetation is restricted to cryptogamic species (Bargagli 2008). Mosses and lichens are the only conspicuous vegetation; however, cyanobacteria and, to a lesser extent, algae are typically the dominant phototrophs in Antarctic soils (Vincent 2002). The complete absence of terrestrial vertebrates means heterotrophic organisms are limited to invertebrates, protozoa, fungi, Bacteria, and Archaea. Antarctic soil communities are, therefore, primarily microbial and appear to be structured almost entirely by abiotic factors due, in part, to extremely limited biotic interactions (Hogg et al. 2006).

The bacterial communities of Antarctic soils have been a focus of many studies since the pioneering work of the 1930s (Darling and Siple 1941). Early-cultivation-based studies successfully isolated and described many bacterial strains (Flint and Stout 1960; Johnson et al. 1978); however, these strains probably represent only the small proportion of bacteria that are amenable to culture (Smith et al. 2006). As a result, Antarctic soils were reported to be depauperate in terms of bacterial abundance and diversity (Flint and Stout 1960), with many soils reported to be sterile (Horowitz et al. 1972). The recent application of molecular techniques has greatly improved the resolution of microbial analyses and revealed that bacterial communities are far more abundant (Cowan et al. 2002) and diverse (Tindall 2004; Smith et al. 2006; Barrett et al. 2006b; Niederberger et al. 2008; Cary et al. 2010) than initially understood.

This chapter summarizes our current understanding of bacterial community diversity and how environmental conditions affect these structures, in soils across the continent. It begins with a brief description of soil distributions in Antarctica using the current terrestrial Antarctic Conservation Biogeographic Regions (Terauds et al. 2012), which are adapted to help structure this review. In the subsequent discussion of bacterial communities in Antarctic soils, an effort is made to present the important environmental features of particular regions to preface discussions of bacterial community characteristics. Finally, the importance of exogenous inputs to bacterial community structures and the temporal responses of bacterial communities to change are examined.



**Fig. 2.1** Map of Antarctica indicating the terrestrial Antarctic conservation biogeographic regions (Terauds et al. 2012)

## 2.2 Continental Distribution of Antarctic Soils

Antarctica's ice-free areas are patchily distributed across the continent. The most recent effort to group these terrestrial areas into manageable conservation bioregions has seen the continent divided into fifteen geographically distinct regions, based on expert opinion and available environmental and biological information (Terauds et al. 2012). As many of these bioregions have not been well characterized microbiologically, it was necessary to adapt the classification system to provide an appropriate means of structuring this review; as a result, the fifteen bioregions have been consolidated here into five regions (Fig. 2.1). Here, the Antarctic Peninsula refers to five biogeographic regions: the South Orkney Islands, North-east Antarctic Peninsula, North-west Antarctic Peninsula, Central South Antarctic Peninsula, and South Antarctic Peninsula. West Antarctica refers to the three biogeographic regions that lie South of the Antarctic Peninsula and West of the Transantarctic Mountains: The Ellsworth Mountains, Ellsworth Land, and Marie Byrd Land. The designation Victoria Land refers to the bioregions South Victoria Land and North Victoria Land. East Antarctica refers to the four biogeographic regions that lie East of the Transantarctic Mountains: Dronning Maud Land, Enderby Land, East Antarctica, and Adelie Land. Finally, the Transantarctic Mountains bioregion is addressed here as its own region.



**Fig. 2.2** Map of Antarctica indicating ice-free areas referenced in this review

Soils between regions can be quite heterogeneous due to variable influences on soil development. Globally, soil development is dependent on five major factors: time, climate, topography, parent materials, and resident organisms (Jenny 1941). Soil properties pertinent to soil biota such as conductivity, pH, nutrient availability, and carbon content are the result of the particular age and development of a soil from bedrock or an emplaced deposit. Antarctic soils are generally coarse-grained sands due to the dominance of physical weathering processes over chemical processes; thus, clays are a minor component of most soils, and nutrient retention and availability are minimal (Campbell and Claridge 1987).

The largest expanses of ice-free land are found in Victoria Land, the Transantarctic Mountains, and the Antarctic Peninsula, while the areas in East and West Antarctica are substantially smaller. To date, microbiological analyses have been most extensively undertaken on the Peninsula and in Southern Victoria Land, while descriptions of bacterial communities in several ice-free regions of the continent are limited (Fig. 2.2).

## 2.3 Bacterial Communities of Antarctic Soils

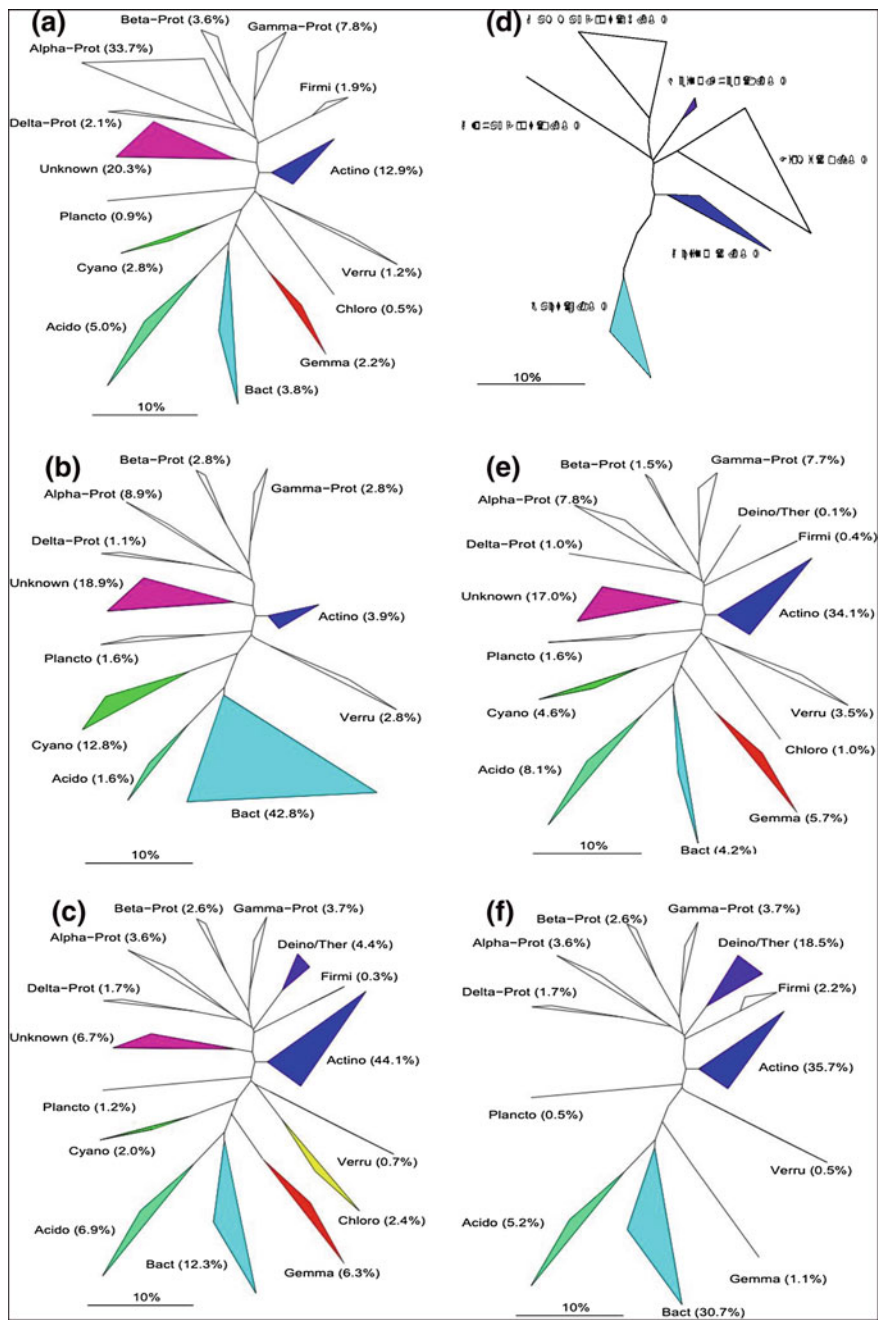
Bacterial community structures of Antarctic soils are highly heterogeneous, though some community characteristics are maintained across many Antarctic soil environments. Several bacterial phyla are frequently observed, including

*Actinobacteria*, *Proteobacteria*, *Bacteroidetes*, *Acidobacteria*, *Gemmatimonadetes*, *Deinococcus-Thermus*, and *Cyanobacteria*, though relative abundances of these groups differ between soils of different regions of the continent (Fig. 2.3). A high proportion of phylotypes observed in culture-independent analyses of Antarctic soils is from unknown or unclassified bacteria, which may reflect that they are unique to Antarctic soils or that similar environments globally have not been well characterized microbiologically (Vincent 2000). Many studies also report dominant phylotypes (Saul et al. 2005; Aislabie et al. 2006b, 2009), in contrast with more even phylotype representation characteristic of temperate soils, which may reflect the harshness of the Antarctic soil environment. That bacterial communities of Antarctic soils can be considered similar by only a few broad features is, perhaps, not surprising, considering the steep environmental gradients that exist both between and within, regions of the continent. Indeed, bacterial communities across Antarctic soils have been found to vary significantly with geography, climate, soil physicochemical parameters, and local biological influences.

### 2.3.1 Antarctic Peninsula

Soils of the Antarctic Peninsula have developed under the most amenable climatic conditions on the continent. With mean annual temperatures ranging from 0 to  $-12^{\circ}\text{C}$  and mean annual precipitation of 200–1,000 mm water equivalent (Balks et al. 2013), these ‘coastal oases’ are exceedingly warm and wet in an Antarctic context. The biology of the Peninsula is also significantly different from that of the interior of the continent, as few invertebrate and plant species found here are shared with other regions of Antarctica (Chown and Convey 2007). The greater availability of water in coastal soils allows significant organic matter buildup, with nutrients generally not limiting plant growth (Balks et al. 2013). Some soils contain up to 10 % carbon in subsurface ‘humic horizons’ as a result of leaching and concentration of organic carbon from overlying biological production (Balks et al. 2013). This is even more advanced in the Peninsular region, where extensive moss peat development is a relatively common feature, with soils formed on peat often being strongly acidic (Balks et al. 2013). The facilitation of more chemical and biological processes allows soil development to progress at a greater rate relative to other areas in Antarctica (though soil development is still weak in a global context) and allows the accumulation, recycling and retention of nutrients to occur. Acid-sulfate soils on King George (Simas et al. 2008) and Seymour Islands (Balks et al. 2013) result from acid production from the oxidation of sulfides and represent an extreme soil habitat as a result of moisture-facilitated chemical weathering.

Bacterial communities have been examined along the entire latitudinal range of the Antarctic Peninsula, allowing trends in diversity and composition to be examined. Bacterial diversity and evenness have been found to decrease with increasing latitude along the Peninsula in unvegetated soils (Yergeau et al. 2007b).





◀ **Fig. 2.3** Phylum level diversity of bacterial 16S rRNA gene sequences from Antarctica. **a** Antarctic Peninsula soils, **b** West Antarctic soils, **c** Victoria Land soils, **d** Ornithogenic soils, **e** East Antarctic soils and **f** Transantarctic Mountain soils. Peninsula soil sequences (1216) are from studies of Signy Island, Anchorage Island, Mars Oasis, Fossil Bluff and Coal Nunatak fellfield and vegetated soils (Yergeau et al. 2007b); West Antarctic soil sequences (180) are from a study in the Ellsworth Mountains (Yergeau et al. 2007b); Victoria Land soil sequences, a total of 426 clone sequences and 25976 pyrosequencing reads, were included from the McMurdo Dry Valleys, from studies in the Miers Valley (Lee et al. 2012; Tiao et al. 2012), Beacon Valley, Wright Valley, Battleship Promontory (Lee et al. 2012), Luther Vale (Niederberger et al. 2008), and Bull Pass and Vanda in the Wright Valley (Aislabie et al. 2006b); ornithogenic soil sequences (514) are from Cape Hallett and Cape Bird in the Ross Sea region (Aislabie et al. 2009); East Antarctic soil sequences (1396) were included from the Larsmann Hills (Bajerski and Wagner 2013) and Schirmacher Oasis (Shivaji et al. 2004); and the Transantarctic Mountain soil sequences (361) were from the Darwin Mountains (Aislabie et al. 2013). The trees were constructed using ARB (Ludwig et al. 2004), with DNADIST and Neighbor joining analysis, and the percentage of sequences in each phyla is shown (*in brackets*). Abbreviations for labels are: *Acido* Acidobacteria; *Actino* Actinobacteria; *Bact* Bacterioidetes; *Chloro* Chloroflexi; *Cyano* Cyanobacteria; *Dein/Ther* Deinococcus/Thermus; *Firmi* Firmicutes; *Gemma* Gemmatimonadetes; *Plancto* Planctomycetes; *Prot* Proteobacteria; *Verru* Verrucomicrobia

This geographical trend explained a greater degree of variation than soil characteristics, suggesting increasingly harsh and unstable climatic conditions are responsible for the observed relationships (Yergeau et al. 2007b). Similar trends with latitude were not observed in vegetated soils, suggesting that effects of climatic stress on bacterial communities are mitigated by the stable temperature, water availability, and nutrient availability conferred by vegetation (Yergeau et al. 2007b). Bacterial abundances may be similarly influenced, as bacterial numbers were found to be enriched in vegetated soils compared with unvegetated sites (Yergeau et al. 2007a).

Across much of the Peninsula, soils are dominated by similar phyla, though several trends with geography and physicochemistry have been reported. The phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Cyanobacteria*, *Proteobacteria*, and *Verrucomicrobia* are frequently observed, and *Proteobacteria* makes up a substantial proportion of soil sequences in the region, with frequent representation of the *Alpha*, *Beta*, *Delta*, and *Gamma* *Proteobacteria* classes (Yergeau et al. 2007b). Microarray analyses have indicated that *Actinobacteria*, *Epsilonproteobacteria*, and *Verrucomicrobia* decreased in relative abundance with increasing latitude, whereas *Cyanobacteria* representation increased (Yergeau et al. 2009) findings that largely corroborated earlier clone-library analyses (Yergeau et al. 2007b). Additionally, clone-library analyses have revealed a significant decrease in *Acidobacteria* representation with increasing latitude (Yergeau et al. 2007b). *Bacteroidetes*, *Firmicutes*, *Cyanobacteria*, and *Alphaproteobacteria* were found to be more abundant relative to other taxa in soils of Fossil Bluff (71°19'S) and Coal Nunatak (72°03') on Alexander Island than at sites on the Falkland Islands, Signy Island, and Anchorage Island (51°76'S–67°34'S) (Yergeau et al. 2009). Several phyla were significantly influenced by soil physicochemical factors, as the proportion of *Chloroflexi* and *Betaproteobacteria* were negatively

correlated with pH, while the proportion of *Firmicutes* and *Verrucomicrobia* were positively correlated with pH (Yergeau et al. 2009). *Chloroflexi* and *Planctomycetes* were positively associated with soil water, organic matter content, and soil nitrogen, and the proportion of *Betaproteobacteria* was positively correlated with soil nitrogen and nitrate (Yergeau et al. 2009).

Soils of Mars Oasis on Alexander Island have been found to be outliers in latitudinal studies of the Peninsula, with higher than expected diversity (Yergeau et al. 2007b). A comparison of soil communities of Mars Oasis, Ares Oasis, and Viking Valley on Alexander Island also found Mars Oasis to have the highest diversity of the three sites (Chong et al. 2011). Soils across the three sites were dominated by *Bacteroidetes*, *Actinobacteria*, and *Acidobacteria*; *Cyanobacteria* were also abundant at Mars Oasis, but below detection limits at the other two locations (Chong et al. 2011). Despite relatively similar representation at the phylum level, few phylotypes were shared between the different soil sites, and variation in community composition was found to be most strongly associated with soil pH and copper content (Chong et al. 2011). Within Mars Oasis, no significant variation in bacterial diversity or community structure was observed in a comparison between two different soils varying in water, carbon, nitrogen, and phosphorous content, suggesting that these parameters have little influence on microbial community structures at this location (Newsham et al. 2010). Newsham et al. (2010) report similar phyla level distributions in soils from Mars Oasis to those found by Chong et al. (2011), though representation of *Proteobacteria* were substantially higher in the former study.

Vegetation has a pronounced influence on bacterial community characteristics in the Antarctic Peninsula. On Livingston Island, *Bacteroidetes* were found to be enriched in moss covered soils compared with the surrounding unvegetated soils, which may be related directly to the plant cover or to the reduced soil pH (Ganzert et al. 2011). On King George Island, rhizosphere soils of the flowering plants *Deschampsia antarctica* and *Colobanthus quitensis* have been found to support similar bacterial communities, and these communities are very different to those reported in unvegetated soils in the region (Teixeira et al. 2010). Rhizosphere soils were dominated by representatives of the phyla *Firmicutes*, *Actinobacteria*, and *Proteobacteria*. The high representation of *Firmicutes* in rhizosphere soils is notable as this group is not found to make up a substantial proportion of the bacterial communities in unvegetated soils of the region (Yergeau et al. 2007b; Teixeira et al. 2010). A high proportion of *Firmicutes* was found to group to the *Clostridia*, suggesting bacterial community structure may be influenced by anaerobic conditions of the rhizosphere.

### 2.3.2 West Antarctica

Ice-free areas make up a small proportion of West Antarctica, at coastal locations in Ellsworth Land and Marie Byrd Land, and at inland nunataks and mountain



ranges that rise above the 500–1500-m-thick ice of the West Antarctic Ice Sheet (Convey and McInnes 2005). Mean annual temperatures range from  $-12^{\circ}\text{C}$  in the vicinity of Russkaya Station in Marie Byrd Land (Abakumov 2010) to approximately  $-30^{\circ}\text{C}$  in the southern Ellsworth Mountains (Dahe et al. 1994). At high altitude sites of West Antarctica, soil is rare and poorly developed (Denton et al. 1992; Convey and McInnes 2005).

Few microbial analyses have been undertaken in the soils of West Antarctica, with the exception of clone-library analyses from soils of the Ellsworth Mountains completed by Yergeau et al. (2007a, b) as part of their latitudinal study of the Antarctic Peninsula. Bacterial community structures were highly dissimilar to those found along the Antarctic Peninsula. Communities were dominated by *Bacteroidetes* of the order *Sphingobacteriales*, which, at 42 % of the sequences observed, more than double the proportion of *Bacteroidetes* observed at any other site in the study (Yergeau et al. 2007b). Additionally, *Cyanobacteria* made up nearly 14 % of sequences in the Ellsworth Mountain clone libraries, which was similar to levels observed in soils of Mars Oasis but substantially higher than all other sample sites along the Peninsula (Yergeau et al. 2007b). Analysis of this data in a continent-wide study of bacterial distributions found the communities of the Ellsworth Mountains were more similar to those on Alexander Island than to those in Victoria Land, despite being located at the similar latitude to the soils of Victoria Land (Chong et al. 2012).

### 2.3.3 Victoria Land

A diverse range of soil types is observed across Victoria Land. Covering a latitudinal gradient of approximately  $8^{\circ}$  and positioned between the polar plateau and the coast, soils in Victoria Land are exposed to a wide spectrum of climatic variation, including variable temperature and precipitation regimes (Barrett et al. 2006b). Desert ecosystems dominate the landscape of Southern Victoria Land and the high altitude areas of Northern Victoria Land, while low-elevation coastal soils of Northern Victoria Land see considerable marine and biological influence (Barrett et al. 2006b). This region also contains geothermal soils on Mount Erebus in Southern Victoria Land and Mount Melbourne and Mount Rittman in Northern Victoria Land.

### 2.3.4 Desert Soils

The McMurdo Dry Valleys of Southern Victoria Land comprise the largest ice-free area on the continent, with approximately  $4,500\text{ km}^2$  of ice-free area (Levy 2013). The mean annual air temperatures ranges from  $-20$  to  $-35^{\circ}\text{C}$ , and mean precipitation ranges from less than 10 to 100 mm (Bockheim and McLeod 2008).

Strong and dry katabatic winds facilitate increased evaporation and sublimation, thus contributing to the aridity of the environment. Considerable salt accumulation in soils high up the valley walls indicates extremely low moisture availability and negligible leaching over long periods of time (Campbell and Claridge 1987). Soil pH is generally alkaline, and carbon and nitrogen contents are typically low except in wetted areas and regions receiving contemporary or legacy organic matter subsidies from nearby high-productivity sites (Elberling et al. 2006; Barrett et al. 2006b).

In the Dry Valleys, any soils of considerable moisture content are patchily distributed and generally concentrated around existing water bodies with ephemeral melt conditions. Soils at the margins of lakes, glacial streams, and ponds are reliant on the short period of the austral summer when liquid water can be sustained (Stanish et al. 2012). Ponds are the most common inland bodies of water and are scattered at all elevations around the Dry Valley system; they are usually small and typically undergo complete freeze/thaw cycles each year relying on snow and ice melt for replenishment (Vincent and James 1996). Lakes are larger inland bodies of water typically with permanent ice cover and a large reservoir of liquid water year round (Howard-Williams and Hawes 2007), and are usually replenished during summer by glacial and snow pack melt water streams (Vincent and James 1996). These streams vary greatly in size and occur with intermittent flow for a few weeks during the summer months (Howard-Williams and Hawes 2007). Within and along the margins of these aquatic systems are microbial (cyanobacterial) mats, which are thought to contribute the most significant primary productivity to the Dry Valleys (de la Torre et al. 2003; Aislabie et al. 2006b).

A large amount of biomass is created by primary production each year within the aquatic systems of the Dry Valleys. This biomass accumulates at the edges of these water bodies where it is freeze-dried and can be blown throughout the valley distributing organisms and providing carbon and nitrogen subsidies to areas of low productivity (Parker et al. 1982; Elberling and Brandt 2003; Moorhead et al. 2003; Nkem et al. 2006; Hopkins et al. 2006a; Barrett et al. 2006b; Wood et al. 2008). The size of these aquatic systems, along with wind intensity and direction, influence the relative contribution of these sources to valley-wide nutrient cycling and productivity (Hopkins et al. 2006a, b). While there is evidence of increased organic carbon with increased proximity to lakes (Elberling and Brandt 2003), ponds (Moorhead et al. 2003), and streams (Aislabie et al. 2006b), similar bacterial and metazoan taxa across geographic latitudes indicate this mat material is also widely dispersed (Barrett et al. 2006a). Stable isotope signatures indicate that carbon and nitrogen in contemporary lake sediments provide the bulk of organic matter to the valleys especially for the contiguous low-elevation areas (Barrett et al. 2006b). Additionally, 'legacy carbon' from ancient lake mats may be an important source of organic matter to soils lacking contemporary primary productivity (Burkins et al. 2000, 2001; Hopkins et al. 2006a).

Other conspicuous sources of organic matter in the Dry Valleys include lithic communities, and mummified seal, and penguin carcasses; however, these sources appear to have more localized influences on soils than microbial mats. Lithic

communities in McKelvey Valley (Pointing et al. 2009) and the Miers, Marshall, and Garwood Valleys (Khan et al. 2011) were found to be distinct from surrounding soil communities, suggesting substantial dissemination of biomass to the local environment is restricted. Similarly, while the presence of an animal carcass at a site may drastically alter the physicochemical parameters and bacterial community composition of the soil, the effects have been found to be restricted to the immediate vicinity of the augmentation (Tiao et al. 2012).

Bacterial community structures in the Dry Valleys vary considerably from those observed in other regions of the continent (Cary et al. 2010). At the phylum level, there is a reduction in the relative abundance of *Proteobacteria* and an increase in the relative abundance of *Actinobacteria* and *Bacteroidetes* in Dry Valley soils compared with those on the Peninsula (Cary et al. 2010). The frequent representation of *Deinococcus-Thermus* and *Gemmatimonadetes* in Dry Valley soils also distinguishes these soils from those with more temperate influences (Cary et al. 2010). These variations are apparent even at the coarse scale of phyla representation, indicating the uniqueness of the bacterial communities in this region.

Within the Dry Valleys, bacterial communities may be highly localized. A comparison of bacterial community structures in soils from similar areas in four valleys (Beacon Valley, Upper Wright Valley, Battleship Promontory, and Miers Valley) revealed variable levels of diversity between valleys, and despite very similar representation of taxa at the phylum level, only 2 of 214 species-level phylotypes observed in the study were shared between all four valleys (Lee et al. 2012). This variability in community composition was best explained by variation in salt content, altitude, and copper content of the soils from the four valleys. These findings suggest bacterial populations may be highly regionalized and challenge assumptions that Antarctic soils may be dominated by a small number of cosmopolitan species (Vishniac 1993).

Much of the variation in bacterial community structures in desert soils of Victoria Land may be linked to water availability. In a survey of soils in Luther Vale, Northern Victoria Land, Niederberger et al. (2008) noted the presence of representatives of the *Deinococcus-Thermus* and *Bacteroidetes* in dry (<4 % soil moisture) low-productivity soils but not in high-productivity soils of higher moisture content (9 % soil moisture). Conversely, *Cyanobacteria*, *Verrucomicrobia*, *Beta-proteobacteria*, and *Gammaproteobacteria* of the genus *Xanthomonas* were found only in the high moisture content soils (Niederberger et al. 2008). In a survey of soils from the Wright Valley in Southern Victoria Land, *Deinococcus-Thermus* and *Actinobacteria* of the genus *Rubrobacter* were also found to be most prevalent in drier soils (Aislabie et al. 2006b). Water content was also found to have an important influence on community composition of stream sediments along the Onyx River of Wright Valley, with *Bacteroidetes* found to be more abundant in wet sediments and *Acidobacteria* more abundant in dry sediments (Zeglin et al. 2011).

In contrast to the findings in Northern Victoria Land (Niederberger et al. 2008), the distribution of *Cyanobacteria* in the Dry Valleys was not found to be related to soil water content (Wood et al. 2008). Community fingerprinting and sequencing were completed using *Cyanobacteria*-specific PCR primers to analyze

distributions in Beacon Valley and Miers Valley soils. Cyanobacterial signatures were below detection or limited to a single phylotype in samples analyzed from Beacon Valley, despite having higher average soil water content than samples collected from Miers Valley, where several phylotypes, grouping to the orders *Chroococcales*, *Nostocales*, and *Oscillatoriales*, were observed (Wood et al. 2008). Variation in cyanobacterial community structures was best explained by differences in elemental composition of soils (Wood et al. 2008).

The similarity of cyanobacterial phylotypes in Dry Valley soils to local lake and hydroterrestrial cyanobacterial mat phylotypes supports suggestions that soils are seeded directly through wind dispersal of mat communities (Aislabie et al. 2006b; Wood et al. 2008). In particular, *Leptolyngbya* spp., which are dominant in microbial mats across the Dry Valleys (Adams et al. 2006), are commonly detected in the surrounding soils (Aislabie et al. 2006b, 2008). Mat samples have been shown to be capable of remaining dormant for many years and returning to activity in the presence of water (Vincent and Howard-Williams 1986), suggesting that windblown mat material not only provides important nutrients to the surrounding soils, but also disseminates potentially active bacterial species throughout the valley floor. The absence of hydrological features (ponds and lakes) in the Beacon Valley compared to Miers Valley was considered an important factor in explaining the differences in cyanobacterial compositions between the two valleys (Wood et al. 2008). Heterotrophic bacteria in microbial mats, which include representatives of the phyla *Actinobacteria*, *Proteobacteria*, *Bacteroidetes*, *Firmicutes*, and *Deinococcus-Thermus* (Brambilla et al. 2001; Van Trappen et al. 2002; Rojas et al. 2009; Peeters et al. 2011), may be similarly redistributed by aeolian processes in Antarctic ecosystems. Indeed, proximity to hydrological features was found to be more important than soil moisture for describing variation in both bacterial and cyanobacterial community structures in Miers Valley soils (Niederberger et al. 2012).

Bacterial community structure and biomass have not been found to vary significantly with variation in metazoan communities in Victoria Land soils (Barrett et al. 2006a). Bacterial community diversity and structure were found to be unrelated to nematode abundance, suggesting there is little top-down control on bacterial communities by these predators (Barrett et al. 2006a). These findings support suggestions that biotic interactions have little influence in shaping Dry Valley soil communities (Hogg et al. 2006), though more detailed studies need to be undertaken to assess the importance of biotic influences.

### 2.3.5 Coastal and Ornithogenic Soils

Low-elevation sites at the northern limit of Victoria Land, such as Edmonson Point (74°S) and Cape Hallett (72°S), can have considerably more developed soils than those found in the Dry Valleys (Hofstee et al. 2006a; Barrett et al. 2006b). Cape Hallett receives annual precipitation of 183 mm of water equivalent per year and has a mean annual temperature of  $-15.3^{\circ}\text{C}$  (Barrett et al. 2006b). Moisture is high

in comparison with other Antarctic soils and can reach saturation during summer (Hofstee et al. 2006b). These northern soils support extensive moss beds, which, together with inputs from sea-bird guano and marine salts, maintain soils of high organic carbon and nitrogen content in relation to soils in Southern Victoria Land (Barrett et al. 2006b).

The presence of large populations of penguins at Cape Hallett, and other coastal areas around the continent, has a pronounced effect on soils. Stone-nest building impacts soil structure, while inputs from penguin guano, feathers, eggs, and corpses result in high organic matter content (Aislabie et al. 2009). Uric acid, derived from penguin guano, is the dominant organic matter, comprising approximately 8 % of soil dry weight (Staley and Henvig 1993). The impacts are so profound that the penguin-impacted soils are classified as ornithogenic soils (Hofstee et al. 2006a; Balks et al. 2013), distinct from all other soil types on the continent.

Bacteria in ornithogenic soils face markedly different conditions to those in surrounding mineral soils. Ornithogenic soils of the Ross Sea region contain similar levels of bacterial diversity to mineral soils in the same region, but differ in abundance and community composition (Aislabie et al. 2009). Culture-based methods estimate bacterial abundances at  $10^5$ – $10^7$  cells/g of dry soil (Ramsay and Stannard 1986), while direct microscopic counts suggest concentrations are closer to  $10^{10}$  cells/g of dry soil (Ramsay and Stannard 1986; Aislabie et al. 2009). *Firmicutes* and *Gammaproteobacteria* of the genus *Psychrobacter* were found to dominate soils colonized by penguins, whereas *Actinobacteria* and *Gammaproteobacteria* of the family *Xanthomonadaceae* were found to dominate soils that had been previously colonized (Aislabie et al. 2009). These differences were attributed to variation in nutrient and salt content of the soil sites, which were higher in colonized soils than in previously colonized soils. The importance of *Psychrobacter* species in ornithogenic soils is supported by culture-based studies of soils from penguin colonies of Magnetic Island in East Antarctica, in which several *Psychrobacter* isolates were found to be halotolerant and capable of utilizing uric acid, or its metabolite allantoin, as their sole carbon and energy source (Bowman et al. 1996). The phylogenetic affiliations of several phylotypes grouping within the *Firmicutes* suggest similar abilities to withstand high salinities and utilize uric acid under anaerobic conditions, which together with the ability of *Firmicutes* to form endospores to withstand environmental stress, would explain their ability to inhabit ornithogenic soils (Aislabie et al. 2009). The dominance of *Actinobacteria* and *Xanthomonas* in previously colonized soils may be the result of a shift in bacterial community structure in response to changing environmental conditions that accompany guano decomposition (Speir and Ross 1984; Zdanowski et al. 2004, 2005) and leaching of ammonium stocks from soils (Aislabie et al. 2009).

### 2.3.6 Geothermal Soils

Geothermal soils exist on the active volcanoes of Victoria Land: Mount Erebus (3,794 m), Mount Melbourne (2,733 m), and Mount Rittman (2,600 m) (Bargagli et al. 1996). Soil temperatures reach 65 °C near fumarolic vents, and soil moisture is sustained surrounding these sites through snow melt and condensation of steam (Bargagli et al. 1996). Steep physicochemical gradients of temperature and pH exist surrounding fumaroles, as demonstrated on Mount Erebus, where soil temperatures were found to decrease from 65 to 3 °C, and pH decrease from approximately pH 7–pH 4, over a distance of 55 cm from fumaroles (Soo et al. 2009).

The geothermal soils of Antarctica's volcanic sites provide the sole oases for thermophilic bacterial communities on the continent. Soils of Mt. Erebus have been shown to support comparable bacterial abundances to geothermal sites in the rest of the world (Hudson and Daniel 1988). Several thermophilic *Firmicutes* (Hudson and Daniel 1988; Logan et al. 2000; Imperio et al. 2008) and *Cyanobacteria* (Melick et al. 1991; Bargagli et al. 1996) have been isolated from Mount Erebus, Mount Melbourne, and Mount Rittman. Much greater diversity, however, was observed in culture-independent analyses of Mount Erebus, which reported representation of the phyla *Acidobacteria*, *Planctomycetes*, *Chloroflexi*, *Cyanobacteria*, *Deinococcus-Thermus*, OP10, and a large number of unclassified bacteria; notably, *Proteobacteria* were not detected in these analyses (Soo et al. 2009). Total bacterial and cyanobacterial community structures were found to be primarily driven by soil temperature and pH (Soo et al. 2009). Geothermal soils are discussed in more detail in this volume in the chapter entitled '[Microbial ecology of geothermal habitats in Antarctica](#)'.

### 2.3.7 East Antarctica

With the notable exception of the Prince Charles Mountains, the ice-free areas of East Antarctica are generally restricted to coastal locations, with the Polar Plateau often sloping right to the coast. The East Antarctic coastline occupies lower latitudes (66–72°S) than the majority of West Antarctica and Victoria Land and lies in a more similar climate band to portions of the Antarctic Peninsula (Balks et al. 2013). This region is considerably affected by marine influences: Soils can be in the order of four times wetter than the Dry Valley equivalents, thus leaching of nutrients and salts is common. Soil pH can be as low as 4 in some areas, ranging through to mildly alkaline (Balks et al. 2013). Landscapes in the East Antarctic oases contain a patchwork of dry soils and 'bogs', arising from the patchy distribution of snow accumulation and subsequent melt (Goryachkin et al. 2004). Moss and lichen cover is considerable in places (Balks et al. 2013) although not in the order of peat-generating beds of the Peninsula.



Several studies have described bacterial communities in soils surrounding the stations operated by various international programmes in the region. Bacterial diversity in a soil from Maitri Station, near Lake Zub, in Schirmacher Oasis has been examined using both culture-dependent and clone-library analyses (Shivaji et al. 2004). Representatives of the phyla *Gemmatimonas*, *Bacteroidetes*, *Actinobacteria*, *Chloroflexi*, *Chlamydiae*, and *Proteobacteria* representing the classes *Alpha*, *Beta*, and *Gamma* were observed in the clone library, with the greatest proportion of sequences grouping to the *Gammaproteobacteria*. Several species of *Proteobacteria* and *Actinobacteria* were also successfully cultured.

Bacterial communities from a range of habitats around Casey Station were analyzed using denaturing gradient gel electrophoresis (DGGE) as a community fingerprinting technique (Chong et al. 2009). Sites included soils that are heavily impacted by human disturbance, soils with low levels of human disturbance, and specially protected sites both formerly and actively colonized by Adelie Penguins. Despite the range of sites sampled, bacterial diversity and community structure were not found to be significantly related to environmental variation (Chong et al. 2009). Sequencing of bands from DGGE gels revealed that majority of bacterial signatures from across all sample sites were from bacterial grouping to the phylum *Bacteroidetes*.

An analysis of bacterial communities associated with glacier forefields in the Larsemann Hills has been completed using a suite of culture-dependent and molecular techniques (Bajerski and Wagner 2013). The study revealed the dominance of *Actinobacteria*, *Acidobacteria*, *Proteobacteria*, *Bacteroidetes*, *Cyanobacteria*, and *Chloroflexi* and several trends in phyla level distributions within the glacial forefield sites (Bajerski and Wagner 2013). *Cyanobacteria*, *Deltaproteobacteria*, and *Gemmatimonadetes* were positively associated with soil moisture and pH, while magnesium, calcium, and potassium were found to influence distributions of *Actinobacteria* (Bajerski and Wagner 2013). *Bacteroidetes* were found to be the most abundant in the vicinity of glaciers, which the authors suggest may be related to low temperature and high water availability at these locations (Bajerski and Wagner 2013). This work provides insight into the process of bacterial succession following glacial retreat and establishes relationships between bacterial community structure and physicochemical properties of soils in the region.

### 2.3.8 Transantarctic Mountains

The Transantarctic Mountains separate the Polar Plateau from the Ross Sea, with ice flow concentrated in major outlets such as the Beardmore and Shackleton Glaciers (see Figs. 2.1, 2.2). At areas where the Transantarctic Mountains exceed altitudes of 1,500–2,000 m, ice-free regions rise above the Polar Plateau. These areas form a discontinuous chain of isolated island-like soil habitats, often separated by expanses of tens to hundreds of kilometers. The high altitude and proximity to the Polar Plateau lead to the most extreme climatic conditions on the

continent. A mean annual temperature of  $-40^{\circ}\text{C}$  and a mean annual water accumulation of only 36 mm per year were estimated from snow pit data at the Beardmore Glacier, Central Transantarctic Mountains (Bockheim 1990). Winds ubiquitously originate from the plateau, and the extreme cold and dryness of this air mass facilitates intense sublimation, exacerbating the influence of precipitation deficiency.

The extreme climate at high altitudes severely depresses soil development, resulting in weakly developed soils even over very long timescales. Soil properties are more homogenous across the Transantarctic Mountains relative to other areas of the continent, as the extreme lack of water precludes many soil development pathways, thereby limiting soil diversity (Claridge and Campbell 1968). With chemical weathering impeded by low water availability, ultraxerous soils are almost exclusively the product of physical processes. Any significant chemical alterations likely indicate an extremely long soil development history. The severe moisture deficit results in dry-frozen permafrost throughout the profile, and ice-cemented soil is generally not observed (Claridge and Campbell 1968). Nutrient levels are low, with organic carbon contents ranging from 0.02 to 0.08 % and organic nitrogen typically below quantifiable levels in relation to inorganic nitrogen content (Claridge and Campbell 2004). In the absence of snow melt and subsequent leaching, atmospheric salts deposited in snow can accumulate to very high concentrations over long timescales (Claridge and Campbell 1968). Salts in far-inland soils are dominated by sulfates and nitrates, relative to chlorides, indicating the influence of the polar air mass rather than marine influence (Campbell and Claridge 1987). A higher sulfate-to-chloride ratio generally correlates with a lower pH; as such, soils on the plateau side of the Transantarctic Mountains are generally less alkaline than those closer to the Ross Sea (Campbell and Claridge 1987).

Recently, cultivation-independent analyses of the bacterial communities in soils of the Darwin Mountains have shown bacterial abundance and composition to be influenced most strongly by soil age and physicochemical properties (Aislabie et al. 2012, 2013; Magalhães et al. 2012). Bacterial community fingerprinting analyses of soils in the Darwin Mountains revealed bacterial diversity was greatest in younger, less developed soils, which had lower salinity and higher C/N ratios than older soils (Magalhães et al. 2012). The authors suggest that salt accumulation in older terrains may constrain bacterial diversity. Additionally, cyanobacterial community fingerprints were examined, and signatures were detected in 57 % of sampling sites, with diversity most strongly correlated with soil pH, C/N ratios, and soil salinity. Interestingly, despite the extremely low water availability in this environment, soil moisture was not found to be a strong determinant of total bacterial or cyanobacterial communities.

In analyses of four drifts in the Darwin Mountains, representing a soil chronosequence ranging from early Holocene (10 ka) to mid-Quaternary (900 ka), phospholipid fatty acids and heterotrophic counts showed microbial biomass to be greatest in less developed soils (Aislabie et al. 2012). Bacterial community structures were found to be influenced by soil development, soil water content,

organic carbon content, and pH (Aislabie et al. 2012), and soil diversity was found to be highest in the least developed soil (Aislabie et al. 2013). Soils were dominated by bacteria grouping to the phyla *Deinococcus-Thermus*, *Actinobacteria*, and *Bacteroidetes* (Aislabie et al. 2013).

Analyses of bacterial communities at locations south of the Darwin Mountains are extending our understanding of bacterial biogeography to the southernmost soils of the continent. Fingerprinting techniques have recently been applied to characterize bacterial and cyanobacterial distributions in soils of the Beardmore Glacier region in relation to soils in the Dry Valleys (Sokol et al. [in press](#)). Distributions of the overall bacterial community were found to be influenced by gradients in pH and soil moisture, while dispersal limitation from aquatic features appeared to have a more important role than environmental gradients in shaping cyanobacterial distributions specifically (Sokol et al. [in press](#)). A combination of bacterial community fingerprinting and high-throughput community sequencing has recently been applied to characterize communities in soils from latitudes 83° to 87°S and preliminary findings indicate significant differences in bacterial diversity and community structures between sites across the region (Scarrow, pers comm).

## 2.4 Exogenous Factors and Inputs

Increased human activity on the continent has the potential to drastically impact bacterial communities, both directly by introducing novel organisms to the environment and indirectly by causing environmental disturbances (Kennicutt et al. 2010). Visitors to Antarctica are exceptional hosts to foreign bacteria and vectors for the transport of organisms to and within the continent (Cowan et al. 2011). A recent study of soils in ice caves on Mount Erebus has indicated potential fungal contamination from human visitation (Connell and Staudigal 2013). Anthropogenic activities in the region also necessitate some level of physical disturbance to soils and increase the threat of chemical contamination to terrestrial and marine ecosystems alike (Kennicutt et al. 2010). Disturbances of terrestrial systems are greatest surrounding permanent settlements; however, even minor levels of activity in sensitive areas of the continent can leave lasting effects on soil communities.

The impacts of the introduction of foreign bacteria to Antarctic soils by human activity remain largely uncharacterized. The harshness of Antarctic soils make them inhospitable to many potential colonizing bacteria (Cowan et al. 2011); however, soils of lower diversity may be more susceptible to colonization by foreign organisms (Van Elsas et al. 2012). While there is evidence of inputs of foreign organisms to Antarctic environments through natural atmospheric processes (Vincent 2000), these exchanges are thought to be restricted by the geographic isolation of the continent and barriers to foreign air masses produced by the Antarctic Circumpolar Current (Pearce et al. 2009). Traces of the human enteric bacteria *Escherichia coli* have been detected in Dry Valley field camps

(Sjoling and Cowan 2000) and the human skin commensal *Staphylococcus epidermis* has been detected through PCR amplification in soils at frequently visited sites (Ah Tow and Cowan 2005). Both *E. coli* (Boyd and Boyd 1963) and *S. epidermidis* strains (Ah Tow and Cowan 2005) have been shown to lose viability quickly in Antarctic soils, suggesting human-associated bacteria have little impact on endemic bacterial communities. However, in light of current climate change predictions, the suggested immunity of the continent to these types of introductions is in question. Given several recent studies showing the local and regional uniqueness of soil microbial communities (Lee et al. 2012; Chong et al. 2012), the transfer of soil bacteria between regions of the continent may be of paramount immediate concern to the biosecurity of the ecosystem as repercussions of such transfers are not yet fully understood (Hughes et al. 2010; Cowan et al. 2011).

Shifts in bacterial communities in response to hydrocarbon contamination have been reported in several Antarctic soils (Aislabie et al. 1998; Whyte et al. 2002; Saul et al. 2005). Soils in the Ross Sea region contaminated with alkanes and polyaromatic hydrocarbons were found to have higher counts of cultureable heterotrophic bacteria and lower bacterial diversity than uncontaminated control soils (Saul et al. 2005). Contaminated soils were dominated by *Proteobacteria* of the genera *Pseudomonas*, *Sphingomonas*, and *Variovorax*, while *Proteobacteria* were found to make up only a minor component of control soils (Saul et al. 2005). These responses are similar to those observed in hydrocarbon contaminated soils of temperate regions (Aislabie et al. 2006a). The breakdown of hydrocarbons in Antarctic soils is extremely slow as biodegradation is largely restricted to the warm summer months (Aislabie et al. 2006a).

Shifts in bacterial community structure may also be induced through physical disturbance of soils. Soils around permanent bases can be intensely disrupted by building and heavy equipment use (Kennicutt et al. 2010), while environmentally sensitive regions can be impacted by foot traffic (Ayres et al. 2008). Trampling has been shown to impact invertebrate species and reduce CO<sub>2</sub> fluxes in Dry Valley soils (Ayres et al. 2008), though specific affects on bacterial communities have not been investigated. Bacterial community structures may be altered by trampling due to disturbance of soil crusts, as has been demonstrated in other cold deserts (Kuske et al. 2012).

## 2.5 Temporal Variation in Bacterial Communities

Recent evidence suggests that temporal variation in bacterial community structure may occur rapidly in response to environmental change in Antarctic soils. In a soil warming experiment on the Antarctic Peninsula, soil community compositions were found to shift in response to an increase of 2 °C over the course of just 3 years (Yergeau et al. 2012). *Acidobacteria* representation was found to decrease in soils of higher temperature, while *Alphaproteobacteria* representation increased. Additionally, warming resulted in a significant increase in bacterial

abundance in vegetated soils. Taxonomic diversity and evenness were not significantly affected by warming; however, functional gene analyses showed a decrease in diversity and redundancy of functional characteristics of soil communities in response to warming.

An experiment in Miers Valley, in which a mummified seal was transplanted to a previously pristine site, showed that bacterial community structure was also altered considerably in just 3 years (Tiao et al. 2012). The augmentation resulted in a significant decrease in bacterial diversity and shifted the community structure from *Actinobacteria* dominated, to *Proteobacteria* and *Firmicutes* dominated. This response was attributed to physical factors, as temperatures were more stable, and relative humidity was both higher and more stable, in soils under the seal carcass than in the surrounding soils.

These studies have important implications for understanding how bacterial community structures may respond to climate change. A continent-wide increase in temperature of 0.12 °C per decade has been observed over the 50 year period from 1957 to 2006 (Steig et al. 2009). Increases in temperature are predicted to continue to drive decreases in snow and ice cover, increases in water and nutrient availability, and increases in vascular plant and bryophyte populations, which have already been reported along the Scotia Arc and Antarctic Peninsula (Convey and Smith 2006). Bacterial communities will likely show rapid and significant responses in structure, activity and diversity to the changes predicted by current climate change scenarios. These may well be the most immediate biological responses to environmental change, making bacterial communities important as early-warning indicators of ecological shifts. What is also clear is that these extreme terrestrial ecosystems harbor unique, locally adapted, microbial communities that may be threatened by climate change. Under the Antarctic Treaty, we have a responsibility to protect this diversity and archive what currently exists for future generations. To this end, New Zealand is pioneering a new Antarctic genetic Archive (AGAr) to capture and preserve Antarctic genetic resources.

## 2.6 Conclusions

The terrestrial ecosystems of Antarctica are influenced by some of the harshest conditions on Earth, resulting in communities that are structured predominantly by abiotic influences. The application of both culture-dependent and molecular techniques has greatly improved understanding of bacterial communities in Antarctic soils, and the degree to which local environmental factors shape community structure. Bacterial communities have been found to be highly heterogeneous between different regions of the continent and within regions, varying primarily with climate and soil physicochemical conditions. However, the current paucity of data from several ice-free areas, coupled with the varied methodologies employed in studies from different locations, severely limits biogeographic interpretations of available datasets.

Increased understanding of the environmental factors shaping bacterial community structure and function is necessary to inform management of terrestrial Antarctic ecosystems and to predict how these regions may respond to environmental change. Microorganisms may well show the most rapid and significant immediate biological responses to climate change, making them important as early-warning indicators of ecological shifts. What is also clear is that these extreme terrestrial ecosystems harbor highly adapted unique microbial communities that may be threatened by climate change, and under the Antarctic Treaty, we have a responsibility to not only protect this diversity but to archive what currently exists for future generations. An immediate response is required by the research community in order to establish bacterial community structure data from across terrestrial Antarctica, as a means of understanding bacterial biogeography and to provide a baseline from which to measure community responses to climate change. To do this, appropriate universal metrics must be established to measure biological change over various timescales, and a concerted effort must be made to bank the current genetic biodiversity, as a resource to monitor change.

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