Don A. Cowan *Editor*

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Physical and Biological Properties of Antarctic Soils

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Chapter 1
Introduction

Don A. Cowan

Abstract Ice-free soils might represent a very small proportion of the total land area of the Antarctic continent, but they harbour substantial and diverse microbial populations. Only since the advent of modern molecular phylogenetic methods has the true complexity of Antarctic soil microbiology been apparent. With this discovery has come a series of 'revelations': Antarctic soil communities are highly structured and physiologically complex, they are important functional components of the different soil systems and they are surprisingly responsive to external variables. There is still, however, much to learn. Many of the phylotypes identified in Antarctic soils belong to the category 'uncultured', so their true roles remain, at best, hypothetical. Virtually nothing is known of the role of some elements of the trophic hierarchy, particularly viruses and phages. Studies of in situ physiologies, process rates and responsiveness to microenvironmental variables are scant. On a macroecological scale, the effects of climate change on microbial community structure and function is largely unknown. That Antarctic soil microbial ecology will remain an exciting focus for research is undeniable. The perception of 'Antarctica as the last pristine continent', the extreme nature of the Antarctic soil habitat, the use of the system as a model for molecular and cellular adaptation, and the growing awareness of Antarctic soil microbes as a unique genetic resource together provide a very strong incentive for continued research development.

1.1 Antarctic Terrestrial 'Soil' as a Microbial Habitat

As defined by the Soil Science Society of America (2008), a soil is

> (i) The unconsolidated mineral or organic material on the immediate surface of the Earth that serves as a natural medium for the growth of land plants. (ii) The unconsolidated

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> mineral or organic matter on the surface of the Earth that has been subjected to and shows effects of genetic and environmental factors of: climate (including water and temperature effects), and macro- and micro-organisms, conditioned by relief, acting on parent material over a period of time.

While this definition is, not surprisingly, rather *phyllocentric*, it does not preclude the inclusion of a diverse range of Antarctic terrestrial 'soil' habitats. The complex geological and glacial history of the continent, the landform structure (with the relatively low latitude peninsula and the high latitude Dry Valleys and exposed subantarctic mountains all contributing ice-free zones), and the proximity to and interaction with marine and terrestrial aquatic habitats, together all present a wide range of soils under this definition. Even the most extreme and apparently depauperate ice-free zones of the Antarctic continent can reasonably be considered as soil habitats, given that all contain microbial populations and detectable, if low, levels of organic carbon.

For a continent which is considered, by much of the world's population, to be little more than an expanse of ice, the presence of oligotrophic, copiotrophic, hyper-arid, water-saturated, permanently frozen (psychrophilic) and locally heated (thermophilic) soils offers scope for an equally diverse range of microbial physiologies and phylotypes.

1.2 Microbial Diversity, Functionality, and Capacity

The past decade has seen a complete revolution in our understanding of the microbial diversity of Antarctic soil habitats. Early culture-dependent studies clearly demonstrated the presence of microbial endemism at the species (and to a lesser extent, the genus) level, but Antarctic soil isolates were restricted to a relatively narrow range of Families, dominated in particular by the Gram-positive Firmicutes. Hindsight now shows that Antarctic soil isolation studies, as for so many other terrestrial habitats, principally targeted the so-called 'microbial weeds'; the fast-growing heterotrophic organisms for which the relatively rich culture media typically employed were not toxic.

The introduction of modern molecular phylogenetic (metagenomic) methods for a more comprehensive analysis of soil microbial diversity has provided some surprising results. The first was that prokaryote diversity was much broader than ever suggested from culture-dependent analysis, with many of the clades found in other soil habitats. By inference (i.e., inferring physiological characteristics from identities), the physiological diversity of Antarctic soil organisms is equally wide (Chan et al. 2013), with many groups identified for which there were, at that stage, no cultured psychrophilic representatives (such as the Acidobacteria and the Verrucomicrobia). The second was that prokaryotic diversity does not follow the accepted latitudinal trends typical for higher organisms (higher latitudes = lower diversity). Data from the east Antarctic Latitudinal Gradient Project (Howard-Williams et al.

2010), where diversity surveys were conducted from Cape Hallett (72°S) to the Darwin Glacier (84°S), show that there were no consistent latitudinal trends, and the local environmental parameters completely dominated larger spatial variables.

As is typical of other soil habitats, certain taxa dominate most Antarctic soil phylotypic datasets: most prominently, the metabolically diverse Proteobacteria and the Actinobacteria (Babalola et al. 2009; Makhalanyane et al. 2013). The prevalence of the latter, particularly the presence of numerous uncultured representatives of the filamentous Actinomycetes, is particularly interesting from a biotechnological perspective, since this group of bacteria has contributed a high percentage of the world's antibiotics. As is now well engrained in the perception of microbiologists, success in phylotypic identification is generally not paralleled by success in accessing these species by classical culturing.

One of the surprising discoveries from the surveys of Antarctic soils has been that while bacterial diversity is high, both fungal and archaeal diversities are unexpectedly low, at least in the arid and hyper-arid soils (Rao et al. 2011). In the identification, in soil samples from the inland McKelvey Valley, of only seven fungal phylotypes, only two of which were affiliated to known genera (*Helicodendron* and *Zalerion*), suggesting that free-living fungi may be more susceptible to environmental extremes than bacteria. It is also notable that Antarctic desert surface soils and soil niche habitats, which are typically aerobic, show few, if any, archaeal taxa, and it is possible that Archaea play a minimal role in soil processes (Pointing et al. 2009).

What has also become clear is that microbial diversity is anything but homogeneously distributed, even in habitats that appear, at least at an observational level such as the Dry Valley deserts, as homogeneous. A recent and very revealing phylogenetic survey of soil samples, from a number of 'geographically disparate' Antarctic Dry Valleys (Lee et al. 2012), shows very distinct regional clustering, with only '2 of 214 phylotypes found in all four valleys.' The significance of this dramatic observation has yet to be fully appreciated, but may become a key factor in helping to understand the drivers of diversity, and in guiding future conservation planning strategies.

It is very evident that a current major gap in our understanding of the composition of Antarctic soil (and many other) communities is the role of viruses and phages (Chap. 5). To date, only a single Antarctic soil phage survey, of saturated Antarctic peninsula soils, has been published (Srinivasiah et al. 2008). This study reported phage densities in the order of $2–6 \times 10^8$ g^{-1}, only twofold-to-tenfold lower than in temperate agricultural and forest soils. Our studies on the Antarctic desert soil metavirome (Zablocki, Adriaenssens and Cowan, unpublished results) show over 80 % unknown sequences, with the known fraction dominated by Caudovirales, with *Siphoviridae* being the most abundant.

There is strong evidence to suggest that most soil bacteriophages exhibit a lysogenic rather than a lytic lifestyle (Williamson et al. 2007) and are therefore largely missed using standard soil extraction and concentration techniques. Single- and double-stranded RNA viruses of lower eukaryotes and some prokaryotes would also not be detected by standard DNA extraction protocols. Given the known numerical dominance of bacteriophages in many ecosystems (López-Bueno et al. 2009; Fancello et al. 2012; Suttle 2007) and their key roles in controlling microbial populations and biogeochemical cycling (Weinbauer 2004; Laybourn-Parry 2009), the paucity of studies on terrestrial Antarctic 'virology' represents a gap in our understanding of the composition and functioning of Antarctic soil communities.

Given the extreme nature of many Antarctic soil environments, with their low nutrient status, very low mean temperatures, and relatively short periods when the combination of temperature and water availability positions the extant communities in the metabolically active zone, it is widely assumed that the contributions of such communities to systems processes (such as C and N turnover) are minimal and that the communities themselves are stable over long time periods. However, there is growing evidence that neither of these assumptions are necessarily well grounded. Various in situ and ex situ functional analyses, including isotope labeling studies and high-resolution respirometry, suggest that core functions are maintained to well below 0 °C and that niche communities such as hypoliths may be important contributors to landscape-scale processes such as dinitrogen fixation.

The rate of change of community composition [as judged using fingerprinting methods such as (*Automated*) *Ribosomal Intergenic Spacer Analysis* (ARISA) which monitors the dominant 20–40 phylotypes in a sample] may be much higher than previously thought. A simple but elegant experiment involving the physical repositioning of a ca. 200-year-old seal carcass from one site to another clearly demonstrated a complete restructuring of the underlying soil community within a 3 year period (Tiao et al. 2012). Irrespective of the exact driver(s) of this change, whether temperature-, water-, light- or nutrient-dependent, the rapid timescale of the change is unequivocal.

1.3 Adapting to the Antarctic Soil Environment

It is accepted without question that survival in the Antarctic environment, by any organism, is a consequence of evolutionary adaptations, expressed at the behavioral, physiological, metabolic, structural, and genetic levels. As an example of behavioral adaptation, Antarctic springtails (such as *Neocryptopygus* sp.) are found most commonly on the ventral surfaces of thin dark rock shards where the surface adsorption of solar radiation presumably elevates the temperature of the underside and increases the potential for mobility and grazing behavior. A similar example of 'behavioral' adaptation might be the propensity for the development of endolithic and hypolithic microbial communities in Antarctic ice-free area where suitable translucent minerals (most commonly sandstone, marble, and quartz) are present (see Chap. 9). In these niche habitats, it is apparent that a combination of factors, including access to Photosynthetically Active Radiation (PAR) and moisture and avoidance of desiccation and physical disturbance, is the driving forces for development (Cary et al. 2010).

At the cellular and subcellular levels, much of our understanding of the physiological and molecular adaptations of Antarctic (soil) organisms to their unique environment comes from culture-dependent studies. While adaptations at the genetic and cellular level are not the focus of this text, and some have been comprehensively reviewed elsewhere (Feller and Gerday 2003; Siddiqui and Cavicchioli 2006; Casanueva et al. 2010), by far, the greatest emphasis has been on thermoadaptation. The evolutionary responses of microorganisms to the potentially damaging consequences of freeze–thaw events, loss of membrane fluidity, and the impacts of Arrhenius Law are reasonably well understood (Hoyoux et al. 2004). The expression of cold shock proteins, the biosynthesis of compatible solutes, the use of thermal hysteresis and ice nucleation proteins, membrane lipid thermoadaptation, and changes in protein amino acid composition are all examples of adaptation to the thermal conditions prevalent in cold environments.

Despite this depth of understanding, the molecular and physiological responses to other Antarctic soil stress elements, such as short wavelength UV radiation, desiccation and low light flux, have received relatively little attention.

Phylogenetic surveys of Antarctic soil prokaryote diversity suggest that certain clades known for their high levels of resistance to desiccation and radiation stress (such as the *Deinococcus-Thermus* clade) are possibly more prevalent than in less ‘hostile’ soil habitats. However, the molecular and genetic basis for such resistance has, at least in psychrophiles, been subjected to only limited research. There is clearly considerable scope for using a ‘systems biology’ approach, including the parallel application of genomics, transcriptomics, proteomics, and metabolomics, to study and understand the basis of adaptation and stress response in single organisms. With the rapid growth of very high-throughput, high-resolution analytical systems (next Generation DNA and RNA sequencing of metagenomes and metatranscriptomes, LC–MS analysis of metaproteomes and meta-metabolomes, microarray systems), it can be confidently predicted that the next decade will see a dramatic rise in whole population analyses, giving detailed information on the range and role of different stress response systems in entire microbial communities rather than the adaptations of single species.

1.4 Threats and Impacts

The Antarctic continent, and particularly the exposed and therefore sensitive soil ecosystems, is perceived to be under threat from two unrelated but potentially substantial threats: climate change (Walther et al. 2002) and human impact (Cowan et al. 2011). That climate change is already affecting the continent is irrefutable—high-resolution terrestrial climate data from over many decades show a dramatic rise in the temperatures of most coastal regions of the Antarctic continent (see Chap. 15, Fig. 15.1), with the Antarctic peninsula being most substantially affected. Due to the limited impact of the circulating waters of the

Antarctic current, the Ross Sea area, which coincidentally harbors much of the ice-free area of the continental surface, is the only region not showing a significant rise in temperature.

The extent and implications of human impact are much less clear, but no less a cause for concern. As detailed by Hughes (Chap. 14), the steady rise in both tourist and research-related activities increases the pressure on the most sensitive habitats of the continent. Physical impacts (chemical spillages, disturbance to sensitive animal and 'plant' communities) are readily observed and measured and are therefore controllable. Other impacts are less obvious and less well understood. There is a growing realization that the presence of human activity leaves a non-indigenous 'footprint', in the form of macroscopic propagules (seeds) and microscopic entities (bacteria and human cellular material). While the former is readily avoidable through the use of good screening and decontamination practices, the latter is virtually impossible to control without imposing highly restrictive operational controls. Although such microbial contaminants may not retain viability in the more extreme soil areas of the continent, such as the Dry Valleys, they are likely to leave a substantial genetic fingerprint (Cowan et al. 2011). Given the prevalent conditions of Antarctic soil environments (cold and dry), these fingerprints may be very long-lived. Virtually nothing is known of the consequences of this nonindigenous biological input, the mobility and transport of the contaminants, their long-term stability, the quantitative and qualitative consequences of horizontal gene transfer, or the consequence of any of these in terms of ecosystem functioning.

1.5 The Way Forward

The soil habitats of the Antarctic continent are diverse, in many ways unique, and have highly restricted dimensions on a global scale and offer huge scope for research into fundamental issues of ecosystems ecology and adaptation. These habitats are not static, to the extent that they have been hugely impacted by the glacial history of the continent, but such changes have been on a millennial scale. Pressure from human activities is, by comparison, a very short-term effect, in that human occupation of the continent is restricted to little more than a century and most significant in the past half century.

The early twenty-first century has seen a growing awareness of the threats to the Antarctic continent. Recent interventions, such as the 2012 50-year Antarctic Horizon Scanning meeting (Chown et al. 2012) and the 2014 SCAR[1]-sponsored Antarctic and Southern Ocean Horizon Scan (http://www.scar.org/horizonscanning/), were aimed at understanding current issues and threats and predicting both their evolution and their consequences. The outputs of these

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[1] SCAR: The Scientific Committee on Antarctic Research (http://www.scar.org/).

deliberations can, at least in theory, be channeled through SCAR, as the international body responsible for Antarctic science policy, to the Antarctic Treaty nations. This process can, as it has done in the past, ultimately influence national and international policies on activities on and around the Antarctic continent.

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Chapter 2
Bacterial Community Structures of Antarctic Soils

Eric M. Bottos, Joshua W. Scarrow, Stephen D. J. Archer, Ian R. McDonald and S. Craig Cary

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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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.

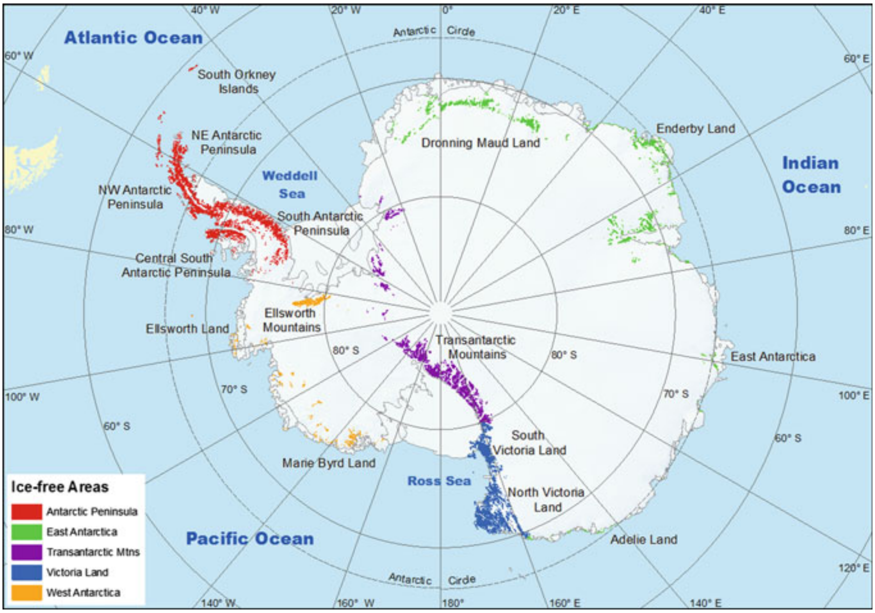


Fig. 2.1 Map of Antarctica indicating the terrestrial Antarctic conservation biogeographic regions (Terauds et al. 2012)

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

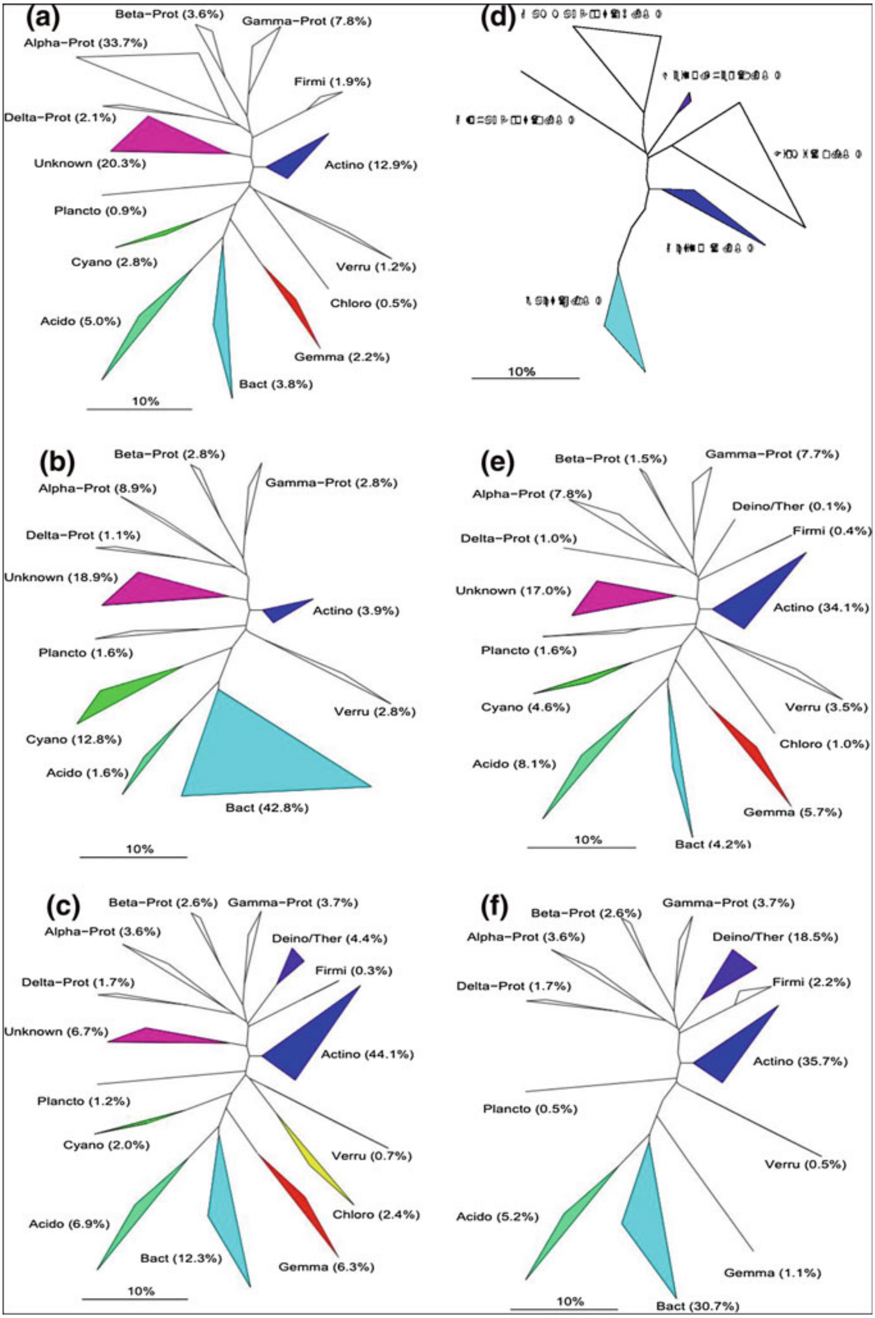
Bacterial community structures of Antarctic soils are highly heterogeneous, though some community characteristics are maintained across many Antarctic soil environments. Several bacterial phyla are frequently observed, including

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 °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).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Gamma-Prot (2.8%)
Delta-Prot (1.1%)
Unknown (18.9%)
Actino (3.9%)
Plancto (1.6%)
Verru (2.8%)
Cyano (12.8%)
Acido (1.6%)
Bact (42.8%)
10%
(e)
Beta-Prot (1.5%)
Gamma-Prot (7.7%)
Alpha-Prot (7.8%)
Deino/Ther (0.1%)
Delta-Prot (1.0%)
Firmi (0.4%)
Unknown (17.0%)
Actino (34.1%)
Plancto (1.6%)
Cyano (4.6%)
Verru (3.5%)
Chloro (1.0%)
Acido (8.1%)
Gemma (5.7%)
10%
Bact (4.2%)
(c)
Beta-Prot (2.6%)
Gamma-Prot (3.7%)
Alpha-Prot (3.6%)
Deino/Ther (4.4%)
Firmi (0.3%)
Delta-Prot (1.7%)
Unknown (6.7%)
Actino (44.1%)
Plancto (1.2%)
Cyano (2.0%)
Verru (0.7%)
Chloro (2.4%)
Acido (6.9%)
Bact (12.3%)
Gemma (6.3%)
10%
(f)
Beta-Prot (2.6%)
Gamma-Prot (3.7%)
Alpha-Prot (3.6%)
Deino/Ther (18.5%)
Delta-Prot (1.7%)
Firmi (2.2%)
Actino (35.7%)
Plancto (0.5%)
Verru (0.5%)
Acido (5.2%)
Gemma (1.1%)
10%
Bact (30.7%)

◀ **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* Bacteriodetes; *Chloro* Chloroflexi; *Cyano* Cyanobacteria; *Deino/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 °C in the vicinity of Russkaya Station in Marie Byrd Land (Abakumov 2010) to approximately −30 °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° 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 km^2 of ice-free area (Levy 2013). The mean annual air temperatures ranges from −20 to −35 °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 course 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*, *Betaproteobacteria*, 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 °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 *Protebacteria* 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 °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_2 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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Chapter 3
Fungal Diversity in Antarctic Soils

Brett E. Arenz, Robert A. Blanchette and Roberta L. Farrell

Abstract Fungi have contributed to Antarctic ecosystems for >200 million years as, from the fossil record, it has been shown that fungi were present in Antarctica since at least the Triassic Period. Fungi have been reported from a wide variety of soils and substrates in far-ranging geographical locations and diverse habitats in Antarctica; the first reports being from as early as the beginning of the twentieth century. In Antarctic studies, non-lichenized fungi have generally been considered separately from lichenized forms and the list of non-lichenized fungi reported from Antarctic regions (including the sub-Antarctic) is extensive at +1,000 species. Fungi are notorious contaminants especially around sites of human activity, and it is crucial to acknowledge the difficulty of discerning transient/introduced versus indigenous and endemic fungi, and to understand their respective contributions to terrestrial biodiversity. To identify fungi, rigorous decontamination procedures on substrates are used along with conventional culturing methodologies and molecular technologies. This chapter focuses mainly on studies concerning terrestrial non-lichenized fungi published since 1993 and highlights specific taxonomic groups that are most important to Antarctic soil ecosystems.

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3.1 Introduction

Research on Antarctic fungi has occurred since the late 19th/early 20th century (Bommer and Rousseau 1905; Brown 1906) and much of the published work on soil microbiology was reviewed in a comprehensive way by Vishniac (1993). The list of non-lichenized fungi reported from Antarctic regions (continental as well as sub-Antarctic islands) is currently freely available for reference online through the British Antarctic Survey (Bridge et al. 2009). Given the number and variety of non-lichenized Antarctic fungal species recorded so far in their extensive review, Bridge and Spooner (2012) suggested that "fungi may be the most diverse biota in the Antarctic". The present review attempts to build upon Vishniac (1993) by focusing on studies published since 1993 and highlighting regional investigations and specific taxonomic groups that are thought to be most important to Antarctic soil ecosystems. The sub-Antarctic Islands are generally not considered in this chapter as those ecosystems are influenced by a more temperate climate. Fungi in cryptoendolithic communities are covered in another chapter in this book (Chap. 9) as well as further detail on fungi found in ornithogenic soils (Chap. 6), and the potential effects of climate change on Antarctic fungal communities (Chap. 13).

3.1.1 Methods for Identification and Detection

Prior to the advent of the polymerase chain reaction (PCR) and more readily available sequencing technologies in the 1980s and 1990s, taxonomic identification of fungal isolates was primarily based on morphological characteristics. This by itself has proven problematic for many fungal clades based on the somewhat subjective nature of these assessments and the high degree of required mycological expertise. It has proven particularly difficult in the case of Antarctic fungi, which in some cases are thought to have lost or reduced morphological defining features (de Hoog et al. 2005) and also rarely produce sexual fruiting structures (Connell et al. 2010; Onofri et al. 2007). In the second decade of the 21st century, identification of fungal isolates is almost entirely based on molecular sequence comparisons. Although this is advantageous in that isolate phylogeny can be compared more objectively between different research groups, it is becoming increasingly clear that identification is dependent on, in some cases, non-curated public databases of dubious reliability (Bidartondo et al. 2008) and the paucity of sequences in general.

Culturing-based studies constituted the bulk of earlier Antarctic mycological investigations. The main advantage of these techniques is that they can be readily adapted to quantify abundances via serial dilutions and a library of isolates can be compiled for further study. The rather glaring disadvantage is that it is estimated only a small percentage of microbial organisms are capable of growing in known cultural media and a substantial bias towards fast growing and frequently sporulating fungi can occur, as plating techniques preferentially count spores over hyphae (Vishniac 1996). Additionally, differing results dependent on the use of selective versus non-selective media and differences in time of year sampled illustrate that a "diversity of methods results in a greater diversity of species being detected" (Wyn-Williams 1996). Techniques that permit isolation of fungal deoxyribonucleic acid (DNA) from total environmental DNA, such as denaturing gel gradient electrophoresis (DGGE) (Arenz et al. 2006; Yergeau et al. 2007a), and direct cloning of DNA fragments have been used to gain a more comprehensive view of Antarctic fungal communities (Bridge and Newsham 2009; Lawley et al. 2004; Jumpponen et al. 2003) with the caveat that the detected organisms may not represent viable organisms. Metagenomic techniques such as pyrosequencing and illumina sequencing and functional genomic studies allow for more comprehensive studies of microbial community composition, abundance, and functionality (Yergeau et al. 2012; Teixeira et al. 2010) yet, to date, studies targeting Antarctic fungi have been few. Though molecular studies have greatly improved community inventories, they are prone to potential PCR and primer bias (Lawley et al. 2004). Truly comprehensive studies of fungal communities should employ both traditional culturing-based studies and molecular techniques in a complementary process.

3.1.2 Cosmopolitan Versus Endemic

A question, which has arisen frequently among Antarctic researchers, is how do we define "native" fungi versus temporary transients? Fungal vectoring can occur over long distances due to atmospheric circulation, birds and animals, and fungi are notorious contaminants especially around sites of human activity. Many species of fungi have great dispersal potential as confirmed, for the Antarctic Peninsula related to specific weather events, by spore trap data (Marshall 1996). In addition, the ability of many fungi to remain in a viable yet dormant spore stage for long periods of time complicates the issue. The practical implication of these concerns is that detection of a particular fungal species in soil or other substrate is often not considered definitive evidence that the species has a true ecological role to play in Antarctica. The presence of "cosmopolitan" species such as *Alternaria*, *Penicillium*, *Aspergillus*, *Cladosporium*, and others are particularly problematic due to their wide dispersal potential and ubiquitous association with human structures and material (Ruisi et al. 2007). Rigorous sterile procedures must be used when sampling to avoid contamination by the sampler. Fungi generally found to be restricted to areas of human activities strongly suggest human introduction (Azmi and Seppelt 1998).

Vincent (2000) postulated that Antarctica would be among the first place to look for microbial endemism, "if microbial endemism (i.e. genotypes of bacteria, protists or other microorganisms specific to a geographical region) is at all possible", given the separation of Antarctica from Gondwanaland >10 million years ago, presence of highly specialized niches, differences in environmental stability, and environmental selection pressure for specific adaptive strategies. However, Bridge and Spooner (2012) concluded that "The great majority of non-lichenized fungi so far described from the Antarctic are cosmopolitan species that also occur elsewhere, and there is relatively little evidence for either local co-evolution or significant numbers of endemic species". Somewhat ironically, it may actually be easier to establish endemism rather than indigenism because a species simply has to be found in Antarctica and nowhere else in the world. Putative endemic status can then be assumed, provided the fungal species is not subsequently found elsewhere in an active role in a non-Antarctic location. Novel fungal species that have been described from Antarctic locations are listed in the attached Appendix.

Establishment of indigenous status (presence AND activity in Antarctica but also in non-Antarctic sites) is actually more problematic as it involves establishing metabolic activity or adaptation. Several criteria (Vishniac 1996) have been proposed to establish indigenous status, as follows:

1. *Visible growth in situ*. This is particularly problematic for Antarctic fungi, which very rarely form macroscopic fruiting structures. An exception is shown in Fig. 3.1, a fruiting body of *Galerina autumnalis*. Mushrooms and other macroscopic fruiting bodies of fungi are not common in Antarctica but they can be found infrequently on the Peninsula.
2. *Occurrence correlations with appropriate environmental variables such as organic matter*. Examples are frequently isolated species from highly specialized substrata, such as the keratinophilic *Geomyces pannorum*, which Vishniac (1996) described as "probably indigenous".
3. *Growth preference of temperatures below 15 °C (psychrophile) and ability to survive freeze thawing*. This may be difficult to determine for reasons discussed in the next section but finding Antarctic isolates with lower temperature preferences than related non-Antarctic strains is at least some evidence of local adaptation.

3.1.3 Temperature Requirements

Most fungi isolated from Antarctic material are cold tolerant rather than true psychrophiles. Cold tolerance, e.g. psychrotrophic, involves capability of growth at around 0 °C (Gerday et al. 1997) but an optimum temperature for growth in the mesophilic range, above 15 °C (Robinson 2001; Vincent 2000). *Hydropisphaera peziza* and *Theobolus microsporus* are psychrotolerant strains of mesophiles isolated from Antarctic soils and adapted to grow at temperatures as low as 1 °C (Azmi and Seppelt 1997). Using the definitions of Morita (1975) and Gounot (1986), true psychrophiles would display maximum growth below 15 °C. It has been speculated that the paucity of true psychrophiles is due to Antarctic soils being dramatically affected by solar warming, and thus, native fungi must be

Fig. 3.1 Fruiting body of *Galerina autumnalis* (Syn = *Galerina marginata*) growing from moss on Amsler Island, Antarctica. Photo courtesy of Carolyn Lipke, Palmer Station, National Science Foundation

adapted to accommodate wide temperature swings. Thirty-five isolates from soil samples taken from a range of locations in Victoria Land between 72°30′S and 77°52′S, including hot soil samples from Mt Melbourne, gave 31 psychrotolerants, two psychrophiles, and one thermotolerant mesophile, demonstrating that within a defined locality, there exists considerable diversity (Zucconi et al. 1996). Robinson (2001) reviewed the subject of fungal adaptations to cold environments, which included abbreviated life cycles, lower saturation of phospholipid membranes, cryoprotectants and anti-freeze proteins, and enzymes that had greater activity at lower temperatures. Lower temperature preferences can also partly be explained by the work of Xiao et al. (2010), demonstrating anti-freeze protein activity in Antarctic fungal isolates, which also were demonstrated to be psychrophiles. Antarctic psychrophilic fungi have been isolated from cryptoendolithic communities (Selbmann et al. 2005; Weinstein et al. 2000) and glacial ice (Turchetti et al. 2011) as well as soils. Psychrophilic yeasts, designated “obvious indigenes”, were isolated from soils and in areas associated with melt streams with visible moss and lichen growth (Vishniac 1996). Xiao et al. (2010) reported a psychrophilic ascomycete species, *Antarctomyces psychrotrophicus*, isolated from the soils of the maritime and continental areas of Antarctica, suggesting a wide distribution of this fungal species in Antarctica.

3.1.4 Limiting Soil Factors

Antarctic soils are a challenging environment for many microorganisms; in addition to being frequently very cold (but subject to wide temperature swings in the Austral Summer) they tend to be highly oligotrophic, relatively saline, and very dry with limited water-holding capacity. Wyn-Williams (1996) described the fundamental importance of microorganisms, including microfungi, to the functioning of Antarctic ecosystems in the absence of macroscopic terrestrial animals. Vishniac (1996) speculated that as fungi are biodegraders and abundant on organic substrata, they have "analagous functions to cyanobacteria in the stabilization and amelioration of the soil structure". Arenz and Blanchette (2011) demonstrated, using 245 soil samples from 18 different locations throughout the Antarctic continent, that fungal abundance was more positively correlated with the percentage of total carbon than any other soil edaphic characteristics; soil moisture was also positively correlated with fungal abundance, while pH and conductivity (salinity) were negatively correlated. Organic carbon in soil is most likely due to input from primary producers whether they be from autochthonous or allochthonous sources, and so fungal abundances and diversity are likely to be strongly influenced by the presence of these organisms in the environment. In the Arenz and Blanchette (2011) study, it was not uncommon for soil samples to yield no culturable fungal organisms, especially from the sites with limited carbon. A related study using introduced sterile wood samples buried in the soil for 2 or 4 years found that the immediately surrounding soil could support significantly higher fungal abundances (1–2 orders of magnitude) than more distant background soils (Arenz and Blanchette 2011). The results of these studies indicated that the oligotrophic nature of most Antarctic soils is the primary factor limiting fungal presence and abundance. Soil characteristics such as nitrogen, pH, salinity, and moisture and climatic factors (temperatures and light regimes) are likely affecting fungi more indirectly through their direct influence on primary producer presence. This trend was also noted by Yergeau et al. (2007a) with soil microbial abundances (fungi and bacteria) significantly associated with location/plant-cover interactions and vegetation-related edaphic characteristics.

3.2 Fungi in the Fossil Record and Glacial Ice

Fungi have been present in Antarctica since at least the Permian period with many examples of diverse fossil fungi being found from the Triassic and Jurassic Periods, as demonstrated by paleomycological and paleoecological investigations (Harper et al. 2012; Stubblefield and Taylor 1983; Taylor and Osborne 1996; Taylor and White 1989). The fossil record from Antarctica suggests the potential relationships that existed were similar to those among the major groups of extant fungi including endogonaceous mycorrhizal associations and wood-decaying fungi, which are widespread today throughout the world (Stubblefield and Taylor 1983; Taylor and White 1989). The presence of fungi in silicified gymnosperm woods (Fig. 3.2) and in peat deposits has provided an important source of information on how these fungi functioned as major decomposers of organic matter, including lignin, for over 200 million years (Kidston and Lang 1921; Stubblefield and Taylor 1983; White and Taylor 1989). Taylor and White (1989) introduced the hypothesis that some of these fungi were likely terrestrial saprophytes, degrading organic materials, and evolving on shorelines and in swamps, where organic materials accumulated prior to the evolution of land plants. Other studies indicated that some fossil fungi were tree parasites and colonized living trees where they exhibited interactions with tyloses and other tree defenses (Harper et al. 2012) or caused wood degradation (Stubblefield and Taylor 1983). The finding of white pocket rot in *Araucarioxylon* and *Vertebraria*, from the Triassic and Permian periods, respectively, demonstrates that fungi with the ability to selectively degrade lignin occurred early in the evolution of fungi and remarkably, had very similar decay patterns to modern day fungi that produce white pocket rots in living trees (Blanchette 1991). Recent molecular clock analyses of 31 fungal genomes representing a wide range of wood-decay basidiomycetes suggest that the ability to degrade lignin corresponds to the end of the Carboniferous period (Floudas et al. 2012). The fossil record from Antarctica appears to hold some of the first evidence of these wood-destroying fungi and their effects on wood.

Fungi have also been found in glacial ice, with fungal spores and hyphae often remarkably well preserved. Taylor et al. (1997) and Ma et al. (2000) described detection and characterization of fungi trapped in glacial ice from Greenland, and the oldest glacial ice from which viable organisms have been recovered was 750,000 years old from Western China (Christner et al. 2003). This work has been extended to fungal recovery in Antarctic ice ranging in age from less than 500 to approximately 200,000 years old, demonstrating that most of the fungi recovered were similar to contemporary fungi, and revealing a higher number of ascomycetes than basidiomycetes (Patel 2006). Additional research that focuses on the ancient fungi trapped in ice is needed to further advance our knowledge on the biology, ecology, and diversity of non-lichenized fungi existing in Antarctica.

3.3 Specific Taxa and Genera

Onofri et al. (2004) reported that in Antarctica, 0.6 % of the known fungal species were water moulds (Kingdom Chromista) and 99.4 % were composed of true fungi including yeasts (unicellular organisms) and filamentous fungi from the phyla Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota. In general, the fungal communities of Antarctic soils are dominated by filamentous ascomycetes with basidiomycete yeasts also a strong component, particularly in the Dry Valleys (Arenz and Blanchette 2011; Connell et al. 2008). Filamentous basidiomycetes have been very rarely isolated (Ludley and Robinson 2008) and even their

Fig. 3.2 Transverse section of silicified *Araucarioxylon*, an ancient gymnosperm, from the Fremouw Peak locality in the Beardmore Glacier area, Antarctica with a white pocket rot caused by a wood-decay fungus. This fossil wood is from the Triassic period and demonstrates the presence of fungi interacting with trees in Antarctica >200 million years ago. Diameter of the fossil wood shown is approximately 7 cm. Photograph by the authors, fossil wood from Thomas Taylor, University of Kansas

typically dominant role as wood-decay fungi in temperate ecosystems has been taken over by ascomycetes in Antarctica (Blanchette et al. 2004b). However, a few filamentous basidiomycetes have been reported including *Sistotrema brinkmannii* found in the Antarctic Dry Valleys (Hao et al. 2010) and *Fibulobasidium* and *Tremella* species on the Antarctic Peninsula (Arenz and Blanchette 2011). Zygomycetes are also isolated with some frequency although not typically as dominant components of fungal communities, with some possible exceptions (Lawley et al. 2004). Chytridiomycota are not frequently reported but were noted to be highly abundant representatives of clone libraries in a specific-site associated with frequent snowmelt (Bridge and Newsham 2009). As they were the dominant components of fungal biodiversity in similarly unvegetated but high elevation soils in Nepal and Colorado (Freeman et al. 2009), it may be that the relative paucity of chytrid isolations has been due to reliance on traditional culturing techniques, which bias against them. Using techniques more specifically designed to target them, Chytridiomycota were isolated from freshwater Antarctic lakes and ponds (Paterson 1973).

Bridge and Spooner (2012) list over 400 fungal genera that have been reported from Antarctic regions (including the sub-Antarctic). However, the list of fungal genera that are reported most frequently from the Antarctic Continent, Peninsula, and immediate surrounding islands can be condensed into a much shorter list.

Ascomycota–Filamentous: *Alternaria, Aspergillus, Cadophora, Cladosporium, Epicoccum, Geomyces, Paecilomyces, Penicillium, Phaeosphaeria, Phoma, Scolecobasidium, and Thelobolus*
Ascomycota–Yeasts: *Aureobasidium, Candida, Chaetomium, Debaryomyces, and Exophiala*
Basidiomycota–Yeasts: *Cryptococcus, Rhodoturula, and Mrakia*
Zygomycota: *Mortierella and Mucor*

3.4 Fungi on the Antarctic Peninsula

The Antarctic Peninsula has a warmer and more humid climate than the rest of continental Antarctica. This is of course partly due to the lower latitude of most of the Peninsula, but it also benefits from a prevailing and relatively warm ocean current impacting from the west. This effect is especially strong on the western coast of the Antarctic Peninsula, which has many more ice-free locations than the eastern coast and has been described as having a maritime climate. These relatively warm and humid conditions allow soils on the Peninsula to support more abundant and diverse fungal communities then other ice-free locations on the continent.

A recent culturing-based study revealed substantially greater fungal species richness in Peninsula soils (0.66 unique Operational Taxonomic Units [OTU] per soil sample) relative to the soils of the Ross Sea Region (0.28 unique OTUs per soil sample) although it must be acknowledged that the Peninsula survey drew from a greater number of sampling locations (Arenz and Blanchette 2011). However, Lawley et al. (2004) also found that maritime Peninsula sites had 3–4 times the fungal diversity than more southerly continental sites.

The Antarctic Peninsula is the only location on the continent that supports vascular plant life, and the two species present, *Deschampsia antarctica* and *Colobanthus quitensis*, are restricted to the Peninsula's northern tip and western coast. The presence of vascular plant life provides fungal niche opportunities unique on the continent. *Alternaria* and *Phaeosphaeria* spp., along with several unidentified ascomycete species, were isolated as endophytes of *D. antarctica* leaves (Rosa et al. 2009). Roots from both *C. quitensis* and *D. antarctica* were found to be colonized by so-called dark septate endophytes (DSE) on the Leonie Islands along the western coast of the Antarctic Peninsula (Upson et al. 2009), among other maritime and sub-Antarctic locations. These DSE isolates were found to be largely composed of fungi from the Helotiales order including the *Leptodontidium*, *Rhizoscyphus*, *Tapesia*, and *Mollisia* genera (Upson et al. 2008).

Although the two species of native vascular plants are restricted to the sub-Antarctic and Antarctic Peninsula, non-vascular plants including mosses and liverworts are more widespread throughout the continent. Mycorrhizal-like infections from *Rhizoscyphusericae* have been noted in the Antarctic liverwort *Cephaloziella variens* (Williams et al. 1994; Upson et al. 2007). Another study on this liverwort noted more ambiguous associations with a number of ascomycete fungi, whose sequences were cloned from the "rhizoid environment" (Jumponnen et al. 2003). Fungi have also been isolated from mosses from locations including King George Island (Moller and Dreyfuss 1996) and fruiting bodies of Agaricales, including *Galerina* and *Omphalia* species, can be found associated with mosses on many of the South Shetland Islands and the Antarctic Peninsula (Fig. 3.1) (authors unpublished data; Guminska et al. 1994; Pegler et al. 1980; Putzke and Pereira 1996). Fungal predators of tardigrades and rotifers, *Lecophagus muscicola*, *L. longispora,* and *L. antarcticus*, are relevant although not strictly soil-inhabiting fungi and they were isolated from sediments and cyanobacterial mats (McInnis 2003). Understanding the ability of these fungi to adapt from one environment to another will assist in determining their ecosystem impact, as McInnis (2003) wrote "Such shallow freshwater sites may represent a physical extension of damp terrestrial habitats as, like the surrounding terrestrial catchments, they freeze solid for up to 9 months each year, and are less influenced by sedimentation and burial processes seen at deeper sites".

As the Antarctic Peninsula extends along a predominantly North–South gradient, it provides an opportunity to test hypotheses related to the ecological effects of latitude, which are often assumed to decrease in biodiversity as distance increases from the equator (Broady and Weinstein 1998). Lawley et al. (2004) tested this hypothesis on six Antarctic Peninsula sites across a range of latitude from 60°S to 72°S with isolates collected over a number of Antarctic field seasons, yet found no significant decrease in eukaryote diversity as latitude and environmental severity increased and that even the most southerly location (Alexander Island) had the highest diversity. Among the six sites studied, 13–38 % of recoverable sequences were from the fungal kingdom. Lawley et al. (2004) also showed limited overlap between the eukaryotic biota of the different study sites, indicating a high level of Antarctic site isolation and possibly endemicity, with ascomycete, basidiomycete, and zygomycete sequences identified. In soils from Signey Island and Coal Nunatuk, the zygosporic sequences dominated.

Yergeau et al. (2007b) utilized a microbial functional gene microarray to assess and compare the abundance of genes critical to microbial-mediated ecological processes between sites on the Antarctic Peninsula and the Falklands Islands and Signey Island. This study found that fungal genes were more highly detected than other sources of carbon decomposition genes at sites on the Antarctic Peninsula, supporting the widely held hypothesis that fungi are the dominant decomposers in these environments.

3.5 Fungi on Ross Island

The exposed soil environments of the Ross Sea Region extend roughly 1,000 km farther south than the central portion of the Antarctic Peninsula. Primary production in this area is largely dependent on scattered patches of moss and lichens, with no documented vascular plants. Ross Island soils are largely composed of volcanic scoria yet due to coastal proximity and marine influences have relatively higher amounts of organic matter deposition than Dry Valley soils much farther inland (Cowan and Ah Tow 2004). Ornithogenic soils around penguin colonies form important sources of carbon inputs to local ecosystems and the fungi associated with these environments are reviewed elsewhere in this book (Chap. 6).

Similar to the Antarctic Peninsula, Ross Island, off the coast of Victoria Land in McMurdo Sound, has significant human impact as it is home to New Zealand's Scott Base and also to the largest Antarctic settlement, the U.S.A. Antarctic Program's McMurdo Station, which hosts a population of some 1,000 researchers and support staff during the Austral Summer. Although changes in the Antarctic Treaty Systems during the 1980s and 1990s led to stricter rules in how Bases and Stations should dispose of their waste and otherwise interact with the environment, the potential for fungal introductions to the continent remains an ongoing concern. In addition to the documented transportation of fungal propagules and soil (Hughes et al. 2010), humans can also influence native fungal communities via the introduction of exotic materials to the continent. Arenz et al. (2010) demonstrated that introduced exotic substrates, which are relatively carbon rich, can initiate large changes in microbial communities in these otherwise oligotrophic soil systems.

Ross Island has had human impact for over a century since it was the base of operations for the early polar explorers, Robert F. Scott and Ernest Shackleton, who conducted the first scientific inquiries in the Antarctic continent and engaged in the "race for the pole" with Roald Amundsen. Many of their wooden structures and artefacts were left behind and are considered an important component of historic heritage from the "Heroic Era" of Antarctic Exploration, 1897–1914. Fungi that are likely indigenous to the local area have been found to be causing a number of serious deterioration issues on these structures and artefacts (Fig. 3.3) and have themselves been the subject of study (Blanchette et al. 2004b; Arenz et al. 2006, 2010; Held et al. 2005; Duncan et al. 2008, 2010; Blanchette et al. 2010; Farrell et al. 2011). These fungi, capable of causing degradation of the historic huts and artefacts, are similar to those present in the soils near the huts and in remote locations; the most frequently isolated genera were *Cadophora*, *Cladosporium,* and *Geomyces* (Arenz et al. 2006) with *Cadophora* also isolated from five out of eight petroleum-contaminated soil samples (Blanchette et al. 2004a) around a historic fuel depot at the Terra Nova Hut, Cape Evans. The latter findings are consistent with the findings of Aislabie et al. (2001) that *Phialophora* (reclassified subsequently as *Cadophora*) was the dominant species in oil-contaminated soil sites in the McMurdo Sound region. In addition, many of these same fungal genera have been found on historic artefacts and

Fig. 3.3 Dark-pigmented fungi growing on a wooden crate from the historic Cape Evans hut built by Robert Scott in 1911. Many of the fungi found in soils of the Ross Sea region have been found colonizing wood and other organic materials brought to Antarctica by the early explorers. Photograph by the authors

structures on the Antarctic Peninsula suggesting a circumpolar distribution (Arenz and Blanchette 2009).

An air monitoring study conducted over 5 years, with summer and winter samplings, testing the interior and exterior areas of the historic huts, demonstrated that frequently isolated soil genera were producing significant aerial spores, with *Cladosporium cladosporiodes*, *Pseudeurotium desertorum*, *Geomyce*s species and *Antarctomyces psychrotrophicus* dominating the air environment of the huts with species of *Cadophora* and *Thelebolus* also isolated (Duncan et al. 2010). Due to the great diversity of *Cadophora* species found in the historic woods, their presence in soils, and dead moss thalli (Tosi et al. 2004), Blanchette et al. (2010) speculated that these *Cadophora* species are likely endemic to Antarctica and not introduced species. An ancestral link between the saprophytic *Cadophora* species currently being isolated from Antarctic soils and organic substrates and the fossilized terrestrial saprophytic fungi proposed by Taylor and White (1989) has been suggested (Farrell et al. 2011).

3.6 Fungi on the Antartic Continent

Victoria Land (which includes the McMurdo Dry Valleys) represents some of the most extreme conditions on the planet, with very dry, cold, highly saline, and low organic content soils (Connell et al. 2008). Yeasts and a variety of fungi have been cultured (Connell et al. 2006, 2008; Vishniac 2006a, b) or detected in these soils, but filamentous fungal abundance was significantly lower in the more inland sites (Connell et al. 2006). Fell et al. (2000) observed an association between basidiomycete yeasts in soils of low moisture content and ascomycetes and zygomycetes in soils with higher water content.

From soils collected from locations in the Transantarctic Mountains (Mount Fleming and the Allan Hills) and Lake Fryxell Basin, Arenz et al. (2006) obtained DNA sequences via DGGE representative of both filamentous fungi and yeasts and similar genera to the soils of Ross Island. However, the only fungi detected using culturing methods by Arenz et al. (2006) from these same soil samples were yeasts such as *Cryptococcus antarcticus*, *C. friedmannii*, *C. vishniacii,* and *Candida parasilosis*. This suggested that the isolated filamentous fungal DNA sequence represented non-viable spores or hyphae. Broady and Weinstein (1998) reported both lichens and filamentous fungi from the La Gorce Mountains (86°30′S, 147°W), a small range in Queen Maud Mountains, which is approximately 350 km from the South Pole. This is the furthest south that mycelia-producing fungi have been reported from open soil environments; however, only four of the 80 collected soil samples yielded fungal isolates even after using a wide range of culturing temperatures. *Cryptococcus* species predominated in most soils, as found in a multivariate analysis of yeast isolates from soil samples on a latitudinal gradient (>77°S to >64°N), including isolates from the Ross Desert (Vishniac 2006b). In this study, the association of *Cryptococcus* yeast species with extreme Antarctic mineral soils was attributed to their polysaccharide capsules, which is thought to contribute significantly to xerotolerance. For almost all sample sites (having determined yeast abundance as well as species identification), 44 % of the distribution of predominant yeast species could be explained by combinations of temperature, precipitation, and electrical conductivity (salinity) (Vishniac 2006b).

During a survey by Connell et al. (2010) of the culturable soil fungal populations in samples collected in Taylor Valley, 13 basidiomycetous yeast strains were isolated belonging to the Dioszegia clade of the Tremellales (Tremellomycetes, Agaricomycotina) but the isolates obtained did not correspond to any previously recognized species with two novel species described, *Dioszegia antarctica* and *Dioszegia cryoxerica*. The latter species typifies some of the aspects earlier cited when studying Antarctic mycology. Although the isolates were notable for producing true hyphae with clamp connections and haustoria, no sexual structures were observed. The two novel species can be considered obligate psychrophiles, since they failed to grow above 20 °C and grew best between 10 and 15 °C.

Pointing et al. (2009) reported the first culture-independent survey of multidomain microbial biodiversity in the high inland McKelvey Valley, and found that landscape-scales and stochastic moisture input had little impact on community structure but in this study, fungi were detected only in endolithic and chamsolithic communities. In a subsequent study of soil samples from McKelvey Valley, Rao et al. (2011) addressed fungal species richness, analyzing total and putative metabolically active assemblages, using environmental DNA and RNA (cDNA), respectively, plus cultivation with a variety of media and selection conditions. A highly restricted assemblage of just seven phylotypes that affiliated phylogenetically within two known genera, *Helicodendron* and *Zalerion* were revealed, with the latter dominating, and none of the commonly found moulds or mitosporic genera observed by other Antarctic investigators were encountered, perhaps as this valley is relatively far inland. The *Helicodendron* species are part of a largely saprophytic family often found on submerged plant debris. *Zalerion* taxa are mostly known from descriptions of marine substrates (Hyde et al. 2000) and this may indicate that a degree of tolerance to saline conditions gave a selective advantage to these fungi in the valleys where soils are appreciably saline as a result of sublimative water loss (Doran et al. 2002), and they have strongly pigmented hyphae which appears important for ultraviolet protection.

Chan et al. 2013 extended the microbial biodiversity study using GeoChip 4, a microarray approach which identifies a broad range of metagenomic ‘potential’ with the most relevant focus on functional ecology. With this approach, they identified in McKelvey Valley both ascomycetes and basdiomycetes with the ability to catabolize complex aromatic compounds.

3.7 Conclusions

The list of fungi isolated from Antarctic soils continues to grow, and more importantly their functional role in the various ecosystems is becoming elucidated. Despite challenges inherent in determining fungal activity and endemism, it is increasingly clear that Antarctic fungi play an important role in decomposition and nutrient recycling and are crucial for soil ecosystem processes. Furthermore, based on the fungal genera that are most frequently identified, it is apparent that specific clades within the Kingdom Fungi differ widely in their ability to adapt to these relatively extreme environmental conditions. Climatic variability, abiotic soil characteristics, presence or absence of primary producers, as well as potential human impacts, all play key roles in determining the composition of fungal communities on the most southern continent. Despite significant advances made in understanding the nature and ecological role of Antarctic fungi, crucial questions remain unresolved. To what extent has gene and genotype flow from more temperate locations impacted the evolution of fungal species in Antarctica? What will be the ultimate effect of human introductions of fungal propagules and exotic substrates on indigenous fungi? And what will be the ultimate impact of predicted climate change on Antarctic microbial communities?

Appendix: Putative Antarctic Fungal Endemics

Apiosodiaria antarctica	Stchigel et al. (2003)
Thielavia antarctica	Stchigel et al. (2003)
Antarctomyces psychrotrophicus	Stchigel et al. (2001)
Cadophora species H37	Blanchette et al. (2004b)
Cadophora species 4E71-1	Blanchette et al. (2004b)
Cadophora species NH1-2	Blanchette et al. (2004b)
Cadophora species 7R16	Blanchette et al. (2010)
Cryptococcus antarcticus	Vishniac and Baharaeen (1982)
Cryptococcus friedmannii	Vishniac (1985)
Cryptococcus victoriae	Montes et al. (1999)
Cryptococcus vishniacii	Vischniac and Hempfling (1979)
Coniobolus antarcticus	Tosi et al. (2004)
Dioszegia antarctica	Connell et al. (2010)
Dioszegia cryoxerica	Connell et al. (2010)
Friedmanniomyces endolithicus	Onofri et al. (1999)
Lecophagus antarcticus	McInnis (2003)
Mrakia psychrophila	Xin and Zhou (2007)

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Chapter 4
Invertebrates

Ian D. Hogg, Mark I. Stevens and Diana H. Wall

Abstract Terrestrial invertebrates are the largest permanent residents for much of the Antarctic continent with body lengths < 2 mm for most. The fauna consists of the arthropod taxa Collembola (springtails) and Acari (mites) as well as the microinvertebrates Nematoda, Tardigrada and Rotifera. Diversity in continental Antarctica is lower compared with warmer regions such as the Antarctic Peninsula and the subantarctic islands and several taxa such as the arthropods have considerably restricted distributions. The highest diversity of invertebrates is found along the Transantarctic Mountains of the Ross Sea Region and taxa are likely to be relicts from a warmer past that have survived in glacial refugia. Dispersal among the extremely fragmented Antarctic landscape is likely to be limited to transport via fresh- or salt-waters, particularly for the arthropod taxa, although long-distance wind dispersal is also possible for the microinvertebrates. Invertebrates possess several adaptations to low moisture levels and extreme cold temperatures in Antarctica. For example, nematodes and tardigrades avoid extreme dry and cold temperatures by entering a desiccation-resistant anhydrobiotic state. In contrast, arthropods do not have such a resistant state and freezing is lethal. Adaptations for the arthropod taxa include freeze avoidance and the production of intracellular, antifreeze proteins. Climate changes in Antarctica are likely to pose significant challenges for the invertebrate fauna. Changes in temperature, soil moisture and associated shifts in taxon distributions as well as the potential for non-indigenous species introductions are all likely to have considerable impacts on the Antarctic fauna. From a conservation perspective, there is a pressing need for terrestrial observation networks to record the present state of Antarctic terrestrial ecosystems as well as to monitor impending changes. Biosecurity measures which minimize species introductions or transfers of organisms within Antarctica will be essential.

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4.1 Introduction

The free-living terrestrial invertebrates are the only permanent, year-round animals found throughout much of the Antarctic continent and consist of two main groups, delineated on the basis of their size, macro- and micro invertebrates. The 'macroinvertebrates' are soil arthropods and consist primarily of mites (Acari) and springtails (Collembola), although chironomid midges (Diptera) are also found in the Antarctic Peninsula (Convey et al. 2008). With the exception of the midges, most individuals are less than 2 mm in length, and as such, are usually considered to be part of the 'mesofauna' (e.g. Coleman et al. 1999). They are also often referred to as 'microarthropods' (e.g. Wallwork 1973; Cannon and Block 1988). In contrast, the smaller 'microinvertebrates' include a range of phyla that are widespread in Antarctic soil habitats including the nematodes, tardigrades, and rotifers and considered part of the 'meiofauna' (Bunt 1954; Jennings 1976; Block 1984). In keeping with the theme of the book, this chapter will focus on the 'true' continental fauna and thus cover only those taxa found in the Ross Sea region of West Antarctica (including the Transantarctic Mountains) and the continental oases of East Antarctica (Hogg and Stevens 2002; see Fig. 4.1)

Springtails and mites were among the first invertebrate animals discovered on the continent, dating back to Discovery Expeditions in the early 1900s. Nematode species were described from samples collected on the Belgian Expedition in the late 1890s and the Discovery Expeditions (see Andrassay 1998). Following these initial discoveries, there was limited work until the late 1950s when extensive efforts were targeted towards cataloguing the diversity of mites and springtails (e.g. Womersley and Strandtmann 1963; Wise et al. 1964; Strandtmann 1967). Work on the microinvertebrates followed with assessments of tardigrades (e.g. Jennings 1976; Dastych 1984; Miller et al. 1988), rotifers (e.g. Dartnall 1983) and nematodes (e.g. Yeates 1970; Timm 1971; Shishida and Ohyama 1986, 1989).

During this latter period, some of the initial ecological and physiological work was also undertaken (e.g. Janetschek 1963, 1967a; Gressitt et al. 1963, 1964; Gressitt and Shoup 1967; Wise 1967). However, by the end of the twentieth century, a range of research activities was underway to expand the descriptions of soil invertebrates, covering several disciplines including physiology, ecology, population genetics and phylogeography. This chapter will focus primarily on this latter period of research and will continue with a description of the currently known continental fauna, as well as their ecology and physiology. We will then consider the origins and phylogenetic relationships of the Antarctic taxa and then conclude with a section on the future and the potential responses of invertebrate populations to environmental changes such as global warming.

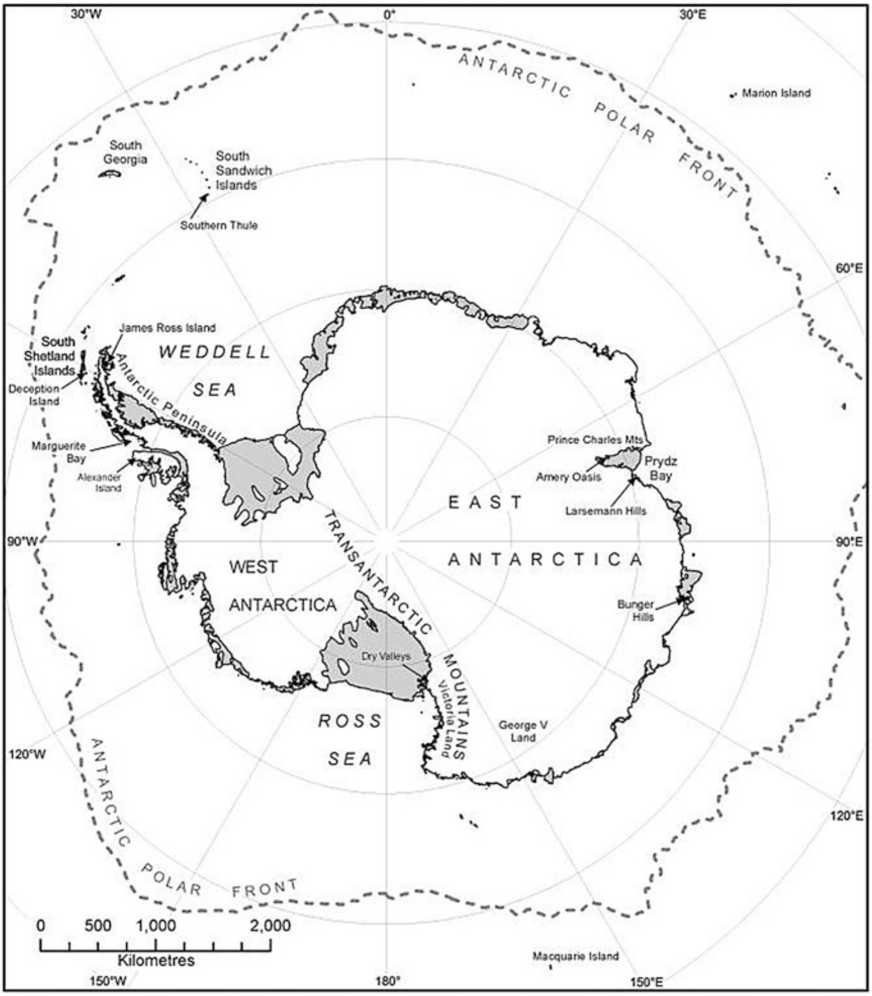

Fig. 4.1 Antarctica including Ross Dependency

4.2 The Macroinvertebrate Fauna

A total of 34 morphologically recognised species of arthropod have been recorded from the Antarctic continent comprising 12 species of springtail and 22 species of mite (Strandtmann 1967; Wise 1971). A complete list of the continental taxa is provided in Table 4.1. For the Collembola, the majority are known only from the Ross Sea region with only three species recorded from the eastern Antarctic coastline (Ohyama and Hiruta 1995) and one species (*Freisea grisea*) is shared between regions. However, molecular data (Torricelli et al. 2010) have suggested that geographically isolated populations on the Antarctic Peninsula are likely to

Table 4.1 The known arthropod fauna from the Antarctic continent including the mites (Acari) and springtails (Collembola). Based on Strandtmann (1967), Wise (1967, 1971), Ohyama and Hiruta (1995)

Taxon	East Antarctica	West Antarctica
ACARI		
PROSTIGMATA		
Nanorchesitidae		
Nanorchestes antarcticus Strandtmann	X	X
N. bellus Strandtmann and Sømme	X	
N. bifurcatus Strandtmann	X	
N. brekkeristae Strandtmann and Sømme	X	
Eupodidae		
Eupodes angardi Strandtmann and Sømme	X	
E. tottanfjella Strandtmann	X	
E. winsnesi Strandtmann and Sømme	X	
Eupodes wisei Womersley and Strandtmann		X
Protereunetes maudae Strandtmann	X	X
Penthalodidae		
Stereotydeus belli Trouessart		X
Stereotydeus punctatus Strandtmann		X
Stereotydeus delicatus Strandtmann		X
Stereotydeus mollis Womersley and Strandtmann	X	X
Stereotydeus shoupi Strandtmann		X
Rhagidiidae		
Coccorhagidia gressitti Womersley and Strandtmann		X
Coccorhagidia keithi Strandtmann		X
Tydeidae		
Tydeus erebus Strandtmann	X	
T. setsukose Strandtmann	X	X
Tydeus wadei Strandtmann		X
Tydeus wilkesi Strandtmann	X	
CRYPTOSTIGMATA		
Maudheimiidae		
Maudheimia petronia Wallwork	X	X
M. wilsoni Dalenius	X	
COLLEMBOLA		
Neanuridae		
Friesea grisea (Schaeffer)	X	X
Isotomidae		
Desoria klovstadi (Carpenter)		X
Cryptopygus antarcticus Willem	X	
Cryptopygus cisantarcticus Wise		X
Cryptopygus sverdrupi Lawrence	X	
Neocryptopygus nivicolus Salmon		X

(continued)

Table 4.1 (continued)

Taxon	East Antarctica	West Antarctica
Gressittacantha terranova **Wise**		X
Antarcticinella monoculata Salmon		X
Antarctophorus subpolaris (Salmon)		X
Hypogastruridae		
Gomphiocephalus hodgsoni Carpenter		X
Biscoia sudpolaris Salmon		X
Onychiuridae		
Tullbergia mediantarctica Wise		X

represent a separate, genetically distinct species compared to the Ross Sea region. The taxonomic status of *Freisea grisea* between the eastern and western continental locations is currently under examination (P. Greenslade and M. Stevens, unpubl. data).

Springtails were some of the first year-round land animals discovered on the Antarctic continent (e.g. Carpenter 1902, 1908), and among the first to be described were the isotomid *Desoria klovstadi*, the neanurid *Freisea gresea* and the hypograstrurid *Gomphiocephalus hogdsoni* (Fig. 4.2). Since then, the latter has been the focus of extensive research covering its distribution, feeding habits, physiology and population genetic structure (e.g. Janetschek 1967b; Davidson and Broady 1996; Sinclair and Sjursen 2001; Stevens and Hogg 2003; McGaughran et al. 2010 and references therein); it is certainly, one of the most studied of Antarctic invertebrates (McGaughran et al. 2011).

Several springtail taxa have remarkably restricted distributions. In particular, *Tullbergia mediantarctica* (Onychiuridae) and *Antarcticinella monoculata* (Isotomidae) are both known from only one or two locations. Interestingly, both species are unpigmented and likely to be traditionally associated with microhabitats deeper in the soil profile (Hopkin 1997). Given the limitations of such habitats in present-day Antarctica, this might, in part, explain their restricted distributions. During the January 2013 field season, a New Zealand team revisited Springtail Point in Southern Victoria Land (Fig. 4.3). This site and much of the surrounding area had not been resampled for Collembola since the initial work of Wise et al. in the early 1960s. Despite extensive sampling of other nearby habitats including Mt Seuss, Mt Gran, and northern Victoria Valley (St. John's Range), *A. monoculata* was found only on an extremely narrow band (<100 m) of scree extending into the Mackay Glacier (Fig. 4.3).

The diversity of mites is more evenly distributed with 14 species in eastern Antarctica and 13 species in the west, of which five are shared between the two regions (Table 4.1). Several mite taxa are known to have relatively wide spatial distributions especially when compared with the springtails. For example, *Nanorchestes antarcticus* is found throughout both Western and Eastern Antarctica (including the Antarctic Peninsula and offshore islands) and along the entire latitudinal gradient of the Ross Dependency (although Sinclair and Stevens 2006 note some doubt in taxonomic identifications over this range). In contrast, *Stereotydeus*

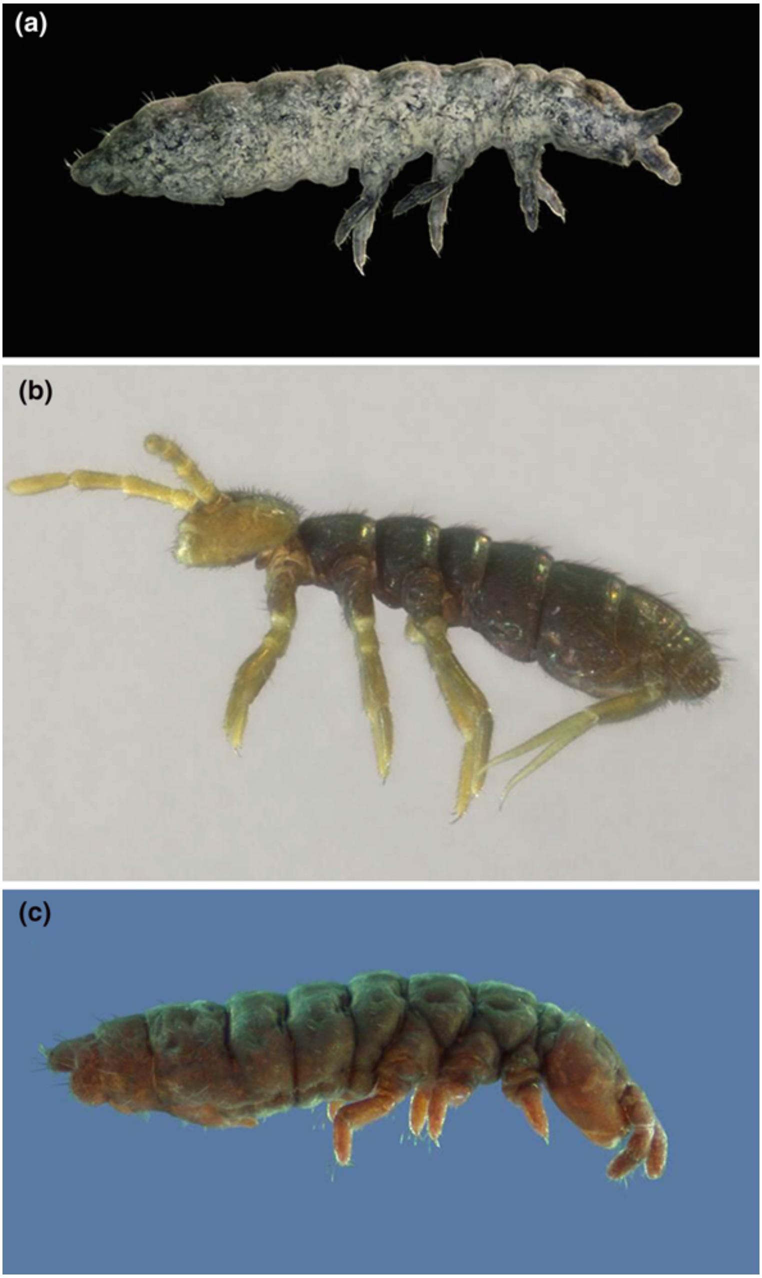

Fig. 4.2 *Freisea grisea*, *Desoria klovstadi* and *Gomphiocephalus hodgsoni* (Collembola) were among the first invertebrates described from the Antarctic continent

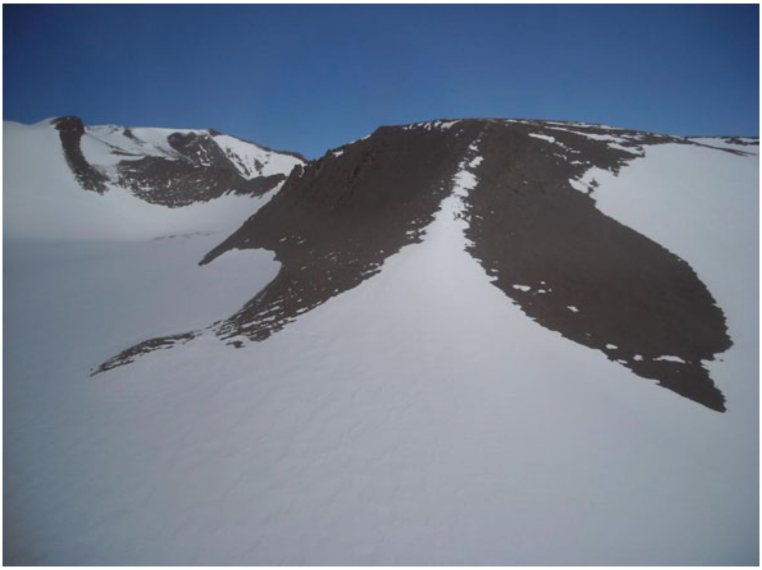

Fig. 4.3 Springtail point in Southern Victoria Land. An example of a habitat with no obvious macroflora (chalikosystem) and containing two species of range-restricted invertebrates (*Antarcticinella monoculata* and *Neocryptopygus nivicolus*)

is represented by five species, some having restricted distributions with *S. belli*, *S. punctatus*, *S. delicatus* found only in northern Victoria Land and *S. shoupi* found in the central and southern Transantarctic Mountains; *Stereotydeus mollis* has a wider distribution in Victoria Land (e.g. Strandtmann 1967; Stevens and Hogg 2002; Demetras et al. 2010) and has also been reported in Eastern Antarctica. However, recent molecular evidence (e.g. Stevens and Hogg 2006; Demetras et al. 2010) has suggested that species-level genetic differences are likely to exist among populations of *S. mollis*. Accordingly, and as per *Freisea grisea*, the status of 'shared' species between the distant geographic regions needs to be viewed cautiously for the macroinvertebrates.

4.3 The Microinvertebrate Fauna

The species diversity of nematodes in continental Antarctica is considerably lower than temperate lower latitude ecosystems, but the number of species varies as new species are described (Sohlenius and Bostrom 2009), genetic and morphological data are examined, and taxonomic classifications resolved. At present, Antarctica has a total of 55 species with 23 species recorded for the continent (see Nielsen et al. 2011 for summary and species list), with the majority being endemic and little overlap between maritime and continental Antarctica (Andrassy 1998, 2008; Andrassy and Gibson 2007).

In the largest ice-free area on the continent, the McMurdo Dry Valleys, *Scottnema lindsayae,* is the most abundant and widespread endemic nematode occurring in drier, saline soils (Wall and Virginia 1999). *Scottnema* frequently occurs as the only invertebrate species in soils, and its distribution occurs as far south as 86°S in the Transantarctic Mountains (Adams et al. 2007) and to East Antarctica (Shishida and Ohyama 1986; Mouratov et al. 2001). The genera, *Plectus* and *Eudorylaimus,* each have three species occurring throughout Victoria Land, and across the continent, although species in these genera may have more restricted distributions. *Plectus* spp. are associated with moss habitats (Simmons et al. 2009) and *Eudorylaimus* and *Plectus* spp. often co-occur in soils of high moisture and organic matter, such as near or in meltstreams or near frozen lakes. Compared to the dominance of *Scottnema, Plectus and Eudorylaimus* in the Dry Valleys, *Geomonhystera antarcticola* occurs rarely and with a patchy distribution and low population densities across the Dry Valleys (Adams et al. 2006; Nielsen et al. 2011). Nearby, in coastal penguin rookeries, *Panagrolaimus davidi* is usually the sole species in the ornithogenic soils (Wharton and Brown 1989; Porazinska et al 2002) and has also been observed across the continent in coastal areas.

Tardigrades and rotifers continue to be described with several new species named since the 1970s (Sohlenius et al. 1995; Convey and McInnes 2005; McInnes 2010). Although usually occurring in moist soil habitats or liquid water (near glacial meltstreams, near lake edges) with communities of nematodes and microarthropods, Convey and McInnes (2005) described five new tardigrade species in a tardigrade-only ecosystem in Ellsworth Land in West Antarctica. This system was especially interesting because the faunal communities showed characteristics of both East and West Antarctica.

More recently, Czechowski et al. (2012) examined continental Antarctic tardigrades using Antarctic and non-Antarctic representatives. They found that comparing known (identified) tardigrades to those collected from the Sør Rondane Mountains (Dronning Maud Land) revealed high levels of sequence divergence that indicated the presence of new species in the genera *Macrobiotus* (Macrobiotoidea) and *Acutuncus* (Hypsiboidea). These levels of sequence divergence compared to morphologically identified species indicated that the diversity of meiofauna in continental Antarctica is underestimated (Czechowski et al. 2012) and molecular techniques have proven a useful indicator (Stevens et al. 2011).

4.4 Ecology

With less than 1 % of the Antarctic continent ice-free (Convey 1997), available habitat is the major factor limiting the distribution of the free-living Antarctic invertebrates. Much of this habitat is also highly fragmented due to the expansive glaciers and ice sheets which cover the continent. This, in turn, provides challenges for inter-habitat dispersal.

Where available habitat does exist, extreme temperatures and limited moisture provide the main ecological constraints on the distribution of biota. These challenges are all particularly relevant for the macroinvertebrates which lack any anhydrobiotic life history strategies commonly employed by the microinvertebrates such as nematodes and tardigrades. The short growing season and potentially limited food options provide additional challenges. Despite these challenges, the few invertebrate taxa which inhabit Antarctica manage to eke out an existence and in some places thrive, attaining densities of several thousand per square metre (Janetschek 1967a).

High levels of incident radiation during the short summer season are readily absorbed in ice-free areas with ground temperatures often around 16–20 °C and higher (e.g. Peterson 1971). Even in the higher latitudes within the Transantarctic Mountains (85^{o}S), Janetschek (1967a) reported temperatures as high as 16 °C. Indeed, our own observations in this same area have recorded soil surface temperatures as high as 20 °C (see also Sinclair and Sjursen 2001a, b). These temperatures are well within the range of temperatures that would be experienced by invertebrates in more temperature regions and are unlikely to provide any major constraints on the growth and survival of invertebrate taxa, at least during the summer period. However, the extreme cold temperatures experienced during winter provide considerable physiological challenges and these will be discussed further in the *Physiology* section below. From a life history perspective, Janetschek (1967b) estimated that *Gomphiocephalus hodgsoni* could complete its life cycle in as short as 38 days. Given the uncertainty of the Antarctic environment, often this will take longer and maybe interrupted during the long winter period. Accordingly, several generations of arthropods are usually observed at any given time or location (Peterson 1971).

The high levels of incident radiation also assist with access to moisture in the form of melt-water from snow packs and glaciers. These provide either running water habitats in the vicinity of glaciers (streams and flush areas) or patches of wet soil near snow packs. This is particularly true for the warmer low-lying coastal areas in both Eastern and Western Antarctica. The largest ice-free area in continental Antarctica is the McMurdo Dry Valleys in Western Antarctica (Fig. 4.5). Here, the Dry Valleys receive extremely low levels of annual precipitation (ca. 2 cm annually) and are among the driest habitats on earth (Hogg and Wall 2012). Nevertheless, suitable habitats for invertebrates exist throughout these areas. For arthropods, moisture is a major constraint as their thin cuticles can result in rapid dehydration. Janetschek (1967a) suggested that relative humidities of >50 % are probably required for the survival arthropods. In terms of soil moisture content, habitats containing Collembola recorded moisture contents of 2–12 % (Janetschek 1967b). Mites are likely to be able to tolerate higher soil moisture content than springtails and are frequently found on wet rocks in the flush zone or margins of, and occasionally in, melt-water streams (Wise et al. 1964; Stevens and Hogg 2002). In contrast, springtails with their hydrophobic cuticles are usually washed away by any running water and are frequently seen floating in eddies of melt streams. A drift net placed in a stream at Granite Harbour in southern Victoria

Land collected roughly 80 individuals in a 24-h period (Hogg and Stevens, unpublished data).

The microfauna, nematodes, rotifers and tardigrades live in water films around soil particles, but the amounts of moisture and relative humidity are not the only factors that define suitable habitats for these organisms. The soil's physical and chemical characteristics (water, pH, carbon, nitrogen, salinity, soil texture) provide soil heterogeneity and a range of soil habitats for life (Magalhães et al. 2012). For example, *Scottnema* and *Plectus* showed varying survival ability to different salts and salt concentrations, complementing previous studies that suggested niche partitioning between the two species in the Dry Valleys (Nkem et al. 2006a, b; Courtright et al. 2001). *Scottnema* has greater abundance in soils with lower moisture, carbon and higher salinity, while *Plectus* is least abundant in those habitats. Nevertheless, co-occurrence of *Scottnema* and *Plectus* exists in some periodically moist soils. The criteria for suitable soil habitats for each species appear to be consistent across the region.

In terms of dispersal among habitats, only limited direct work has been undertaken and most of the information is based on indirect or anecdotal accounts. Among the most obvious of dispersal methods for flightless invertebrates would seem to be via wind dispersal. For microinvertebrates such as nematodes and tardigrades, which can enter a desiccation-resistant anhydrobiotic phase, wind dispersal may provide a viable means of moving between habitats. Supporting this notion are molecular genetic data collected from the nematode *Scottnema lindsayae* which suggest that populations in the Dry Valleys (76^{o}S) and from the Beardmore Glacier vicinity (84^{o}S) are genetically similar (Adams et al. 2007). Further evidence for long-distance dispersal comes from nematodes rehydrated from dry soil accumulated in wind particle collectors placed throughout Taylor Valley (Nkem et al. 2006a, b). Active nematodes, tardigrades and rotifers are also dispersed by water across landscapes such as when permafrost and glaciers melt (Nielsen et al. 2012). For arthropods, with their thin cuticles and propensity for desiccation (Janetschek 1967a), long-distance wind dispersal seems unlikely. Nevertheless, dispersal of arthropods on a local scale as a result of wind is likely. More probable means of long-distance dispersal for arthropods include rafting (e.g. Hawes 2011) as well as the possibility of bird-mediated transport (e.g. Stevens and Hogg 2003). It is well known that springtails are hydrophobic and readily float in freshwater and marine habitats. Hawes et al. (2008) provided experimental evidence demonstrating that the Antarctic springtail *Cryptopygus antarcticus* can survive for long periods (>22 days) 'rafting' on their shed exuviae (skins) in marine and freshwater environments and can even obtain nourishment by using this as a food source. Similarly, McGaughran et al. (2011) demonstrated that *G. hodgsoni* could survive for extended periods in salt water. No direct evidence for bird-mediated dispersal has yet been provided. However, anecdotally, springtails from Cape Bird on Ross Island and Granite Harbour were genetically identical (Stevens and Hogg 2003), and that this corresponds to the moulting behaviour of local Adelie penguins. Birds from a large colony at Cape Bird swim to Granite Harbour at the end of each season and moult before returning to the sea for winter.

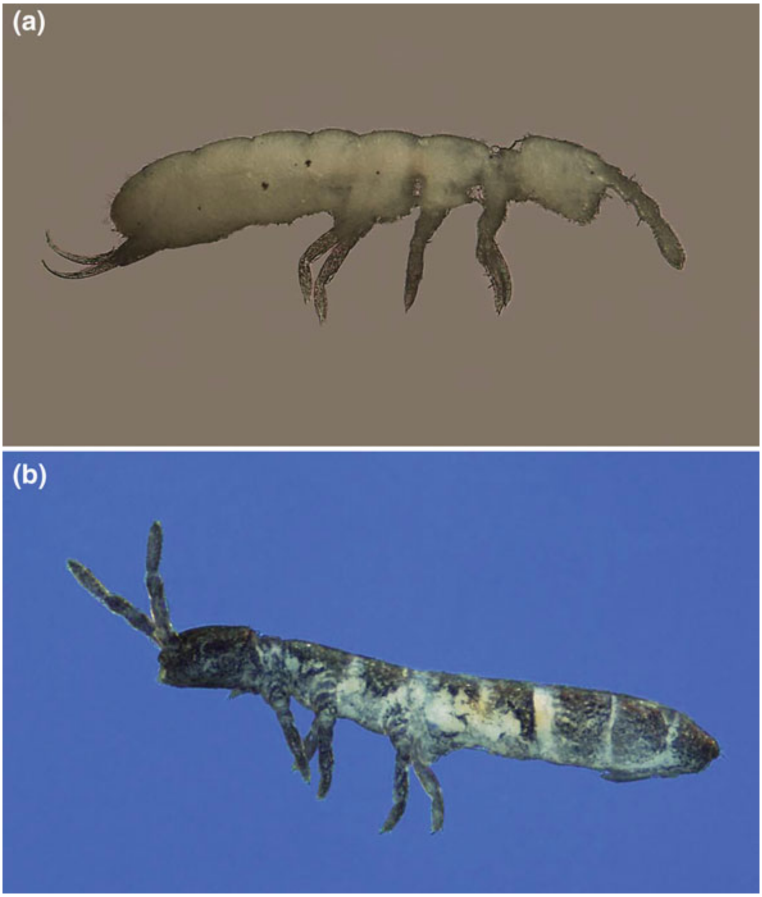

Fig. 4.4 *Antarcticinella monoculata* and *Neocryptopygus nivicolus* (Collembola), examples of range-restricted invertebrates found at Springtail Point (shown in Fig. 4.3)

Antarctic skua are also known to move readily between the two areas. Accordingly, one possible explanation for the genetic similarity is the transfer of individuals via bird-mediated dispersal between the two locations.

The soil ecosystems found in Antarctica are often thought to be one of the few examples where biotic interactions such as competition and predation are absent (Janetschek 1967a) and the system is driven primarily by abiotic factors (Hogg et al. 2006). This is perhaps an oversimplification and a consequence of looking at incorrect spatial or temporal scales (Caruso et al. 2009). Regardless, they are certainly among the simplest of soil ecosystems in terms of numbers of trophic levels in the soil foodweb (Wall 2005). From an invertebrate perspective, this limits the range of available foods and in the absence of predation, means that most taxa rely on primary productivity. Based on the availability of primary producers, Janetschek (1963) split terrestrial habitats into two main types: ones which have obvious moss and lichen growth (bryosystems) and those lacking such obvious growths (chalikosystems). In these latter habitats, food is restricted to the microflora and consists primarily of algae. Decomposers such as bacteria and fungi are common to both. Bacteria are food sources for several nematode species across the continent, such as *Chiloplacus*, *Scottnema*, *Panagrolaimus* and *Plectus*, but evidence is lacking for competition as few of these species co-occur, each having well-defined soil habitat characteristics (Wall 2005).

Given the limited range of food items available, competition would seem likely particularly between taxa which occupy similar habitats. The limited studies of feeding habits for various species suggest that this is also possible. For example, green algae and fungi were reported as part of the diets of *Nanorchestes* and *Stereotydeus* (Gressit et al. 1964; Fitzsimons 1971a). Davidson and Broady (1996) found that *G. hodgsoni* also had a similar diet, with perhaps a heavier reliance on fungal food sources. All three species *S. mollis*, *N. antarcticus* and *G. hodgsoni* are often found in the same locations. Interestingly, the more widespread *G. hodgsoni* is not found at Springtail Point where soil samples were found to have high algal densities (Wall unpubl. data) and that two other species of springtail (*A. monoculata* and *Neocryptopygus nivicolus*, Fig. 4.4) co-occur. This suggests, at least anecdotally, that the species have different dietary requirements which may limit competition. Knowledge of dispersal mechanisms, availability of food sources and soil characteristics all contribute to understanding suitable habitats for each species and, in turn, species ranges.

4.5 Physiology

Tolerance of the extreme winter temperatures experienced by invertebrates necessitates physiological adaptation. There are three broad considerations, namely how these adaptations have developed on evolutionary time scales leading to differences in cold tolerance abilities (see Addo-Bediako et al. 2000) that influence the ability of an organism to respond to climate changes; seasonal time scales of the order of summer–winter (see Bale 2002; Somme 1999) and the physiological changes throughout these seasons; and, short-term time scales whereby invertebrates track temperature changes in their microhabitat (see Sinclair et al. 2003b). The study of cold tolerance has developed over the last three decades, in particular rapid cold hardening (RCH) and supercooling points (SCP), the point at which an organisms body fluids freeze, can be lowered by removing ice nucleators from the gut and accumulating carbohydrate antifreeze compounds (Cannon and Block 1988; Sinclair et al. 2003a). It has become apparent that the responses of invertebrates to temperature are dynamic and include changes to cold tolerance in response to other (non-cold) stresses, changes in freezing survival, and shifts in SCP distributions (see also Sinclair et al. 2003a, b).

Overwinter and diurnal survival in continental Antarctica for terrestrial invertebrates is of particular interest to understand the physiological processes and strategies adopted but also have direct implications on interpretations on species antiquity in Antarctica (see next section). The physiology of cold adaptations in general is well understood in ectothermic invertebrates (Block 1990; Block et al. 2009; Sinclair et al. 2003a). Ectotherms face several dangers of freezing from seasonal and diurnal exposure to subzero environmental temperatures and the steps to avoid or embrace ice formation in their bodies comes from four basic strategies: (1) Anhydrobiosis—extensive dehydration that removes all free water from an organism so that there is no water left to freeze; (2) Vitrification—solidification of water into an amorphous glass state in order to circumvent the physical and osmotic injuries caused by water freezing into ice crystals; (3) Freeze avoidance—deep supercooling of body fluids achieved with the use of multiple kinds of antifreezes; and (4) Freeze tolerance—the controlled freezing of body water in extracellular fluid spaces while preserving the liquid state of the cytoplasm. The first two strategies are primarily used by microfauna or life stages such as eggs or cysts.

The complexities within each of these strategies are becoming clearer, although freeze-tolerant groups appear to contain complexities not well understood (see Sinclair 1999; Sinclair et al. 2003a, b). Terrestrial habitats, despite 24-h daylight during the summer, have strong diurnal cycles in temperature (Worland and Convey 2001; Sinclair et al. 2003b; Stevens and Hogg 2006) and terrestrial invertebrates not only have to survive the long cold/dark winter but also these daily fluctuations during summer. To date there are little data on the winter conditions they must endure, especially in the less accessible continental Antarctic and the studies of invertebrates from the Northern Hemisphere are essentially ‘poles apart’ (Sinclair et al. 2003a).

Mites (Acari) and springtails (Collembola) are both able to survive low temperatures by utilising freeze-avoidance strategies, whereby freezing would be lethal, but is avoided by lowering the freezing point of the animal to below the ambient (environmental) temperature (Block 1990; Block et al. 2009). Numerous studies have been undertaken to characterise the lower lethal temperature of mites and springtails by measuring the SCP, although only few have been undertaken on Antarctic continental species.

Cryptopygus antarcticus from the maritime Antarctic (also known from East Antarctica) has been intensively studied with regard to cold tolerance. Supercooling points for *C. antarcticus* during the summer tend to be in the ‘high group’ (>−15 °C) (Somme and Block 1982), but acclimation to low temperatures show lower supercooling points, with the ‘low group’ means in the region of −24.5 °C (Somme and Block 1982) to −26.5 °C (Somme 1978). *Cryptopygus sverdrupi* has also been studied from isolated nunataks in Dronning Maud Land, which show that the summer mean supercooling point of −28.6 °C reduced to −34.6 °C following acclimation with −38 °C the lowest supercooling point for this species (Somme 1986). Somme (1986) reported accumulation of large quantities of glycerol during acclimation experiments, while Somme and Block (1982) reported a multicomponent cryoprotectant system comprising glycerol, mannitol and trehalose in *C. antarcticus* from the maritime Antarctic.

Pryor (1962) reported that individuals of another continental Antarctic isotomid species, *D. klovstadi*, could survive periods at temperatures as low as −50 °C although no quantitative data exist to suggest a mechanism for this exceptional cold tolerance and it is not supported by a more recent study (Sinclair et al. 2003b). Sinclair et al. (2003b) examined diurnal variation in SCP of three species of Collembola in northern Victoria Land and showed different strategies to microclimate temperature variation. This may not be surprising given the taxonomic relatedness among the three species and that likely explains the difference between the single Neanuridae (*Friesea grisea*) and two Isotomidae (*D. klovstadi*, *Cryptopygus cisantarcticus*) species which revealed diurnal changes in SCP (but all above −30 °C). Perhaps more significant is that the microhabitat preferences between these species, diet and behaviour, for example whereby *D. klovstadi* likely avoids lower night-time temperatures by vertical migration, a behavior that has also been documented for *G. hodgsoni* (Stevens and Hogg 2006) and *N. nivicolus* (M. Stevens unpubl. data).

For *G. hodgsoni* in southern Victoria Land, Block (1985) reports SCP of around −30 °C during late November–mid-January, while −28 °C (Janetschek 1963) and −23 °C (Fitzsimons 1971a, b) have also been reported. More recently, mean SCPs ranged from −35.4 °C in October (with high glycerol content) to −28.3 °C in January (low glycerol content), with the lowest SCP measured at −38.0 °C (Sinclair and Sjursen 2001a). Quantities of glucose and trehalose were low during October, but steadily increased throughout the summer. Haemolymph osmolality was exceptionally high at the end of November, but this rapidly declined by late December (Sinclair and Sjursen 2001a). There was a strong relationship between glycerol content and SCP, but the relationship between haemolymph osmolality, SCP and carbohydrates was uncertain. Nevertheless, *G. hodgsoni* must undergo some further cold hardening beyond the level observed in late October in order to survive the very low temperatures in exposed habitats. The physiology of this species during the winter and during the summer–winter transition still remains to be investigated.

Although mites appear to be phylogenetically constrained to a freeze-avoiding strategy, a number of species of polar and temperate mites have also been shown to survive very low temperatures by avoiding freezing, although there are few examples from continental Antarctica. Fitzsimons (1971a), (b) made some measurements of thermal limits of *S. mollis* during one summer, reporting lower lethal temperatures between −11 and −23 °C. However, no direct measurements of cold tolerance were made, and sampling dates were not reported. Block (1985) measured supercooling points of mites from a number of locations during a single summer season and made a division of animals into high or low groups (SCP above or below −20 °C, respectively), reporting mean low group SCPs between −24 and −28 °C, while Sjursen and Sinclair (2002) report an SCP of −29 °C. They suggest that behavioural mechanisms (for example, microhabitat selection) may allow species to avoid potential stress of freezing temperatures. However, to date, cold-hardiness and ecology of *S. mollis* have only been studied during summer (Gressitt and Shoup 1967; Fitzsimons 1971a, b; Block 1985; Sjursen and Sinclair 2002), and nothing is known about its overwintering strategy. Summer SCPs below −30 °C have not been recorded (summer absolute minimum recorded was −31.7 °C; Sjursen and Sinclair 2002), yet winter soil surface temperatures, even beneath snowpack, are shown to be below this temperature, and can approach −40 °C (Sinclair and Sjursen 2001a). Clearly, considerable physiological acclimatisation to survive, varying strategies of different life stages (i.e. eggs) or microhabitat selection to avoid these temperatures must occur to allow *S. mollis* to persist through the winter, as is the case for Collembola.

In a theoretical framework, the question of whether freeze-tolerance, freeze-avoidance, or a mixed strategy represents the best adaptation for overwintering ectotherms to endure severe winter has been examined (Voituron et al. 2002). The results showed that the freeze-tolerance strategy is strongly dependent on a low sensitivity to the number of freezing days and on a capacity to reduce stress associated with freezing. This strategy is also favoured when the initial energetic level is low compared to the freeze-avoidance strategy, which is favoured by a high initial energetic level, a low stress associated with the supercooling, and a low sensitivity of this strategy to climatic conditions. The mixed strategy permits survival in harsher environments but requires the optimisation of all parameters involved in both cold-hardiness strategies. However, the mixed strategy shows energetic advantages in variable environments allowing animals to resist the harshest periods. From the model results, it appears that the physiological processes developed by ectotherms to reduce these stresses might be a key to understanding the evolution of the cold-hardiness strategies (Voituron et al. 2002). However, one important element that appears lacking in assessments of such adaptations has been an organism's metabolism.

Terrestrial ecosystems in Antarctica are characterized by substantial spatial and temporal variation at several levels encompassing both the organismal and the ecological (e.g. Sinclair 2001; Adams et al. 2006; Chown and Convey 2007). In particular, temporal variation among individuals is strongly linked with phenotypic plasticity, which appears prevalent in Antarctic terrestrial species and may be driven by environmental unpredictability (Chown and Convey 2007). Indeed, life histories of terrestrial taxa tend to be dominated by responses to the seasonally variable, stressful environment (Convey 1996) in conjunction with the low Antarctic energy budget. Environmental constraints such as large daily microhabitat temperature fluctuations during summer (>30.8 °C) and long periods of limited resource availability are reflected in terrestrial arthropods by slow growth rates and extended life cycles compared to their temperate counterparts (Convey 1996).

Metabolic studies of terrestrial Antarctic Collembola are particularly limited to early work, which focused on *C. antarcticus* (Block and Tilbrook 1975, 1978), and the metabolism of continental Antarctic arthropods remained unstudied until recent years with the first clear evidence of intraseasonal variation in standard metabolic rate for a polar terrestrial invertebrate (McGaughran et al. 2009b, 2010). McGaughran et al. (2009b, 2010) found a relationship between metabolic rate and microclimatic drivers and identified that metabolic rate in *G. hodgsoni* is not simply a direct function of temperature, because the decreases demonstrated during later measurement periods occurred while mean microhabitat temperatures had increased. This provides the first strong implication that systematic metabolic rate variation in the terrestrial environment may be related to intrinsic energetic requirements—in this case with elevated metabolic activity coinciding with that portion of the summer season during which important life history functions such as replenishing nutritional status after the depleting Antarctic winter takes place. The possibility of systematic variation in metabolic rate over time within an individual organism in response to specific energetic requirements remains difficult to assess. Metabolic rate elevation alone merely imposes an increased energetic cost on the organism and, in the absence of comparable rate elevation in other key processes, will simply result in an increased rate of resource depletion (Convey 1996). Hence, an important requirement for the advancement of understanding of metabolic rate variation lies in identifying its functional consequences for terrestrial biota.

It is clear that the life history strategy of Antarctic terrestrial arthropods such as *G. hodgsoni* is governed by a matrix of factors (both biotic and abiotic) (see Hogg et al. 2006). Over temporal scales, both intrinsic seasonal variation and local microhabitat conditions clearly have strong influences on metabolic rate variation, including potentially setting restrictive limits on activity very early in the season. From a spatial perspective, metabolic rate variation may be caused by differences among populations in mass, energy assimilation and expenditure (i.e. MCA), climatic and habitat differences and/or a combination of other factors including genetic variability and its relationship to fitness. In addition, a suite of other factors that in some cases remains difficult to quantify and/or account for (e.g. diet, developmental stage, sex, thermal history, hydration status) may be important influences of both spatial and temporal (particularly over winter) patterns of physiological variability. Studies to isolate and quantify these factors are clearly required.

Microinvertebrates such as nematodes, rotifers and tardigrades can endure extreme changes in soil habitat microclimate. These can be for long periods (days to months) covering seasonal extremes of both summer and winter, or over shorter periods (minutes to hours) in summer due to desiccating winds, variable temperatures, low soil moistures and relative humidities. Taxa having several physiological responses such as both cold and desiccation tolerance in response to changing abiotic conditions are well adapted to the Antarctic, polar desert, conditions (Wharton 2003; Treonis and Wall 2005, Block et al. 2009; Adhikari et al. 2010). Several intensive studies have explored the differing survival strategies of soil nematodes that occupy distinct soil habitats of southern Victoria Land. *P. davidi*, a coastal nematode species not only survives intracellular freezing (freeze tolerance), but has other physiological mechanisms to survive cold temperatures (see Wharton 2003; Block et al. 2009 for reviews). In field studies of dry soils of Taylor Valley dominated by *Scottnema lindsayae*, nematodes respond to drying conditions by coiling, an indication of anhydrobiosis (Treonis and Wall 2005). When soil moistures were less than 2 %, (gravimetric) approximately 80 % of the nematodes were coiled and inactive and uncoupled from their food source and transfer of nutrients. More recently, laboratory studies of *Plectus murrayi,* a soil nematode, associated with mosses in Dry Valley ephemeral meltstreams in the summer (Courtright et al. 2001; Simmons et al. 2009) examined gene regulation of survival to drying and freezing. The results showed that suites of genes are differentially expressed in response to different environmental stresses and adaptations to dehydration stress also promote survival to freezing. Interestingly, a slower desiccation in *P. murrayi* can enhance the lower limits of freeze tolerance.

Tardigrades and rotifers respond to desiccation slowly and, like nematodes, alter their morphology and their biochemical pathways to produce antifreeze compounds (Wright 2001; Ricci 2003). Both rotifers and tardigrades reduce surface area by folding to a 'tun'-like shape (Leasi et al. 2009). Tardigrades have an added protection in that wax is extruded from the cuticle and reduces surface transpiration. Tardigrades of many species and from different habitats besides the Antarctic have been shown to be freeze-tolerant with a potential to super-cool (Hennegherr et al. 2009). They survive best with a faster cooling rate (Hennegherr et al. 2009). Leasi et al. (2009) showed that rotifers entering anhydrobiosis reduce their body volume and compact their internal organs into the body chamber. These and other changes protect overall structure and prevent biological membranes from being disrupted.

4.6 Origins/Phylogeny

Terrestrial organisms throughout the Southern Hemisphere that have circum-Antarctic distributions have generally been used to examine hypotheses that test between ongoing dispersal (by wind, water, or migrating birds) or relict Gondwanan distributions. Few of these have extant representatives in Antarctica, but such taxa contribute to our understanding of the evolutionary origins of the continental Antarctic fauna. Either these taxa have survived the harsh climate cooling in Antarctica over the last 23 Myr (Gondwanan/vicariance origin) or they have dispersed there more recently. What has sparked this interest has been paleological studies that reveal the continental landscapes of the Antarctic were dominated by Nothofagus-herb-moss tundra vegetation during more moderate climates that persisted until possibly the late Miocene (12–7 MYA) or Pliocene (7–2 MYA) (Ashworth and Cantrill 2004). The fossil record suggests that terrestrial (e.g. weevils and flies) and limnetic faunas (e.g. lymnaeid gastropods, bivalves and freshwater fish) persisted until the late Miocene or Pliocene (Ashworth and Cantrill 2004). It remained unclear how much, if any, of the terrestrial Gondwanan fauna survived the glaciation of Antarctica through to the present (Wise 1967; Brundin 1970).

This question did not receive further attention until studies started to examine the origins of Antarctic fauna using molecular data (see reviews by Convey and Stevens 2007; Convey et al. 2008, 2009), but unfortunately studies with adequate sampling to test this hypothesis are few and only examine Collembola, mites and tardigrades. There is now good evidence that much of the continental Antarctic terrestrial fauna are remnants rather than recent (post-LGM) arrivals. Stevens et al. (2006, 2007) and McGaughran et al. (2010) examined six species of continental Antarctic Collembola while Stevens and Hogg (2006) examined the mite *S. mollis*. The overriding pattern found was that the diversification of arthropods is likely to have occurred as a result of the glaciation and isolation of the Antarctic continent completed by around 12 MYA and not by the sequential break up of Gondwana (completed by 32 MYA) or more recently during repeated glacial cycles of the Pleistocene (2 MYA). This implies the continuous presence of refugia on ancient continental landmasses with appropriate environmental conditions. Species' distributions and the diversification of arthropods have revealed how global climate change may have influenced Antarctic biodiversity. The evolutionary history of these continental Antarctic arthropods reflects a diverse origin of both vicariant (Miocene) isolation and dispersal through time.

Recently, Czechowski et al. (2012) was the first to examine any continental Antarctic meiofaunal group using Antarctic and non-Antarctic representatives. They found that the tardigrades from the Sør Rondane Mountains (Dronning Maud Land) revealed high levels of sequence divergence that indicated that the Sør Rondane Mountains have been isolated for a considerable period. The deep levels of sequence divergence indicated that populations on relatively close nunataks within the same mountain range have been separated and isolated, with limited population exchange over a significant period with lack of connectivity to outside Antarctica at similar timescales as previously found for the arthropods (Czechowski et al. 2012).

4.7 The Future

Antarctica is undergoing dramatic climate changes that will affect the communities of terrestrial soil fauna that we have discussed thus far. For example, rapid temperature changes currently being experienced (e.g. Fig. 4.5) are expected to have profound effects on the resident biota. In response, there have been several research papers, book chapters and special issues of journals that have addressed potential effects of climate changes on the terrestrial soil fauna of Antarctica (Sinclair and Stevens 2006; Wall 2007; Nielsen et al. 2011; Hogg and Wall 2011, 2012; Wall 2012). The response of biota to these changes will be varied and dependent on a number of factors, several of which will be synergistic.

Many of these species have existed for thousands of years under the cold, dry, isolated conditions and have developed special adaptations to exist in their specific habitats. The dispersal of individuals through newly available corridors (e.g. via exposed ground or meltwater) has the potential to disrupt locally adapted gene complexes that are the product of Antarctica's dynamic evolutionary past. Of

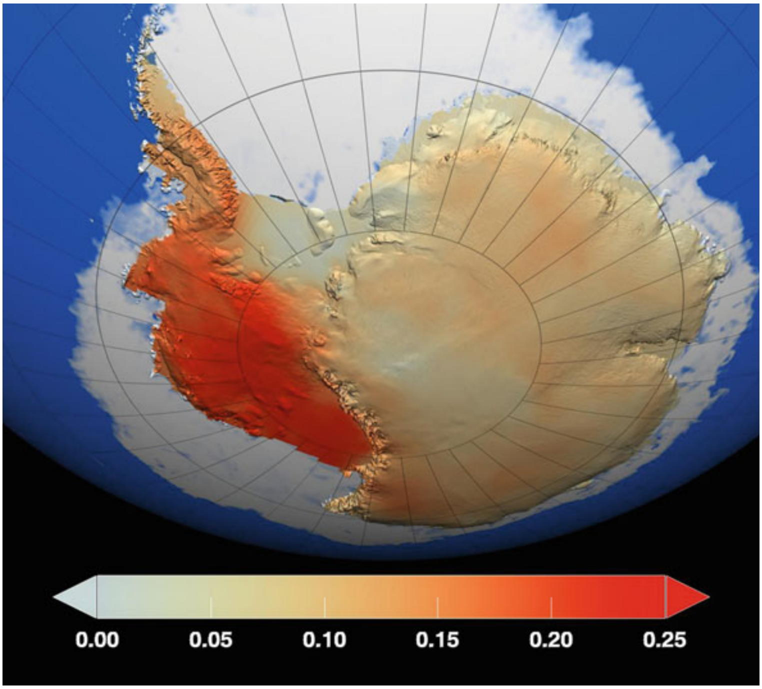

Fig. 4.5 Colour image of Antarctica showing temperature changes that have occurred within the past 50 years. Of note are the rapid changes occurring in the area encompassing Western Antarctica (*darker red* sections)

further concern is the introduction of non-indigenous species to Antarctica (sensu Chown et al. 2012).

Our intent in this chapter has been to discuss our current knowledge of the continental fauna which might help to inform environmental models predicting whether species ranges will retract or expand in response to climatic changes and species introductions. For example, ‘climate envelope’ models use the identity of species, their distributions and their physiological responses to various environmental conditions to describe the range of suitable conditions needed for the species to live in the future.

However, our knowledge of species and their tolerance to climate extremes, and thus our projections of how ecosystems will respond to climate change, is based on those sites that are easily accessible to researchers, near national research bases or coastal areas (Wall 2007). There has been much less research on species towards the interior of Antarctica, where ice-free nunataks and valleys exist. Recommendations calling for establishment of terrestrial observation networks have highlighted and justified the need to increase exploration and monitoring of the biota (Wall et al. 2012). A major concern now is the need to collect data on how warming of glaciers and permafrost will affect various ecosystems, including how species will survive warming, how species will assemble into new communities, and how 'new' ecosystems will establish and function with, as yet, unknown species. Areas that may be particularly informative to climate changes are ecotones—transitions between one ecological type to another—where shifts to different ecological states are likely to be most pronounced.

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Chapter 5
What Do We Know About Viruses in Terrestrial Antarctica?

D. W. Hopkins, M. M. Swanson and M. E. Taliansky

Abstract Very little is known about viruses in soils and, given the small number of studies on Antarctic soils, it is unsurprising that definitive information about viruses in Antarctic soils is sparse. The occurrence of unusual virological observations (novel virus, dual virus sequences, virophage, and large phage to host ratios in Antarctic soils) suggests that substantial unexplored detail exists for viruses in Antarctic soils.

5.1 Introduction

Viruses are the most abundant biological entities in the biosphere. In marine and soil habitats, the number of virus particles exceeds the number of cells by at least an order of magnitude (Casas and Rohwer 2007; Edwards and Rohwer 2005; Suttle 2005). Numerous viruses infect organisms from all branches of cellular life. Approximately 2,300 different viruses are currently recognized by the International Committee on the Taxonomy of Viruses (King et al. 2011), but the majority of these have medical, veterinary, or crop plant pathological importance, or are viruses with biotechnological significance. The number of recognized viruses is certainly a massive underestimate of the real diversity because of the likely diversity in unscreened potential hosts and the many natural environments that have been either scarcely sampled or not sampled at all (Breitbart and Rohwer 2005; Fierer et al. 2007). Despite the evidence, sometimes indirect, for the abundance and diversity of viruses, very few natural habitats have been sampled or

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examined systematically, but recent metagenomic analyses are starting to reveal previously unknown diverse assemblages of viruses in air, soil, and water samples (Angly et al. 2006; Dinsdale et al. 2008; Fierer et al. 2007; Kristensen et al. 2010; Srinivasiah et al. 2008; Suttle 2007; Williamson et al. 2005, 2007). Given the limited knowledge of viruses in natural habitats and the suspected large abundance and diversity, it is not surprising that Fierer et al. (2007) reported that the majority of the approximately 4,500 virus-related nucleotide sequences found in soils showed no similarity to previously described sequences and that there was little taxonomic overlap for the viruses between sites, indicating both high local and high global diversity.

In this chapter, we outline what is known about terrestrial Antarctica virus ecology, summarize the small number of reports on the viruses in Antarctic terrestrial environments, highlight examples of new and unusual observations for viruses from Antarctica, and provide some insight from recent screening of soils from the dry valleys of the abundance and diversity of viruses. In this way, our opening question “What do we know about viruses in terrestrial Antarctica?” is addressed, and although our knowledge is sparse, it is important to note that Antarctica has yielded new insights from a very small number of studies. The investigation of viruses in Antarctica as a whole and in terrestrial habitats in particular is in its infancy, and the literature base is comprised of mostly isolated reports. This makes generalizations and the identification of ecological patterns and processes difficult. About a decade ago, Pearce and Wilson (2003) reviewed ecological aspects of viruses in Antarctica with an aquatic bias because of the relative abundance of aquatic studies. We have drawn heavily on this review, but we provide a particular focus on terrestrial Antarctica and have included additional information that has flowed from the application of molecular and metagenomic approaches to virus ecology since Pearce and Wilson’s (2003) review.

For the purposes of this chapter, we have included some information on viruses in the populations of marine mammals and birds found in coastal regions, and zoonotic viruses which can transfer between humans and Antarctic animals because of the relevance to conservation of the Antarctic biota. We have also covered some information about viruses in aquatic habitats because they are likely to be sources of viruses arriving in terrestrial habitats. We do not cover research on virus disease transmission between human populations in Antarctica, even though this was probably the first virological topic ever reported from Antarctica (the putative infection of Amundsen’s party with the common cold when visited by Scott’s Northern party in the Bay of Whales in February 1911).

5.2 Animal Viruses

Except for the coastal regions of continental Antarctica and the maritime Antarctic, where marine mammals and birds come ashore periodically mostly for reproduction and nesting, the Antarctic fauna is exclusively comprised of invertebrates, dominated by arthropods and nematodes in drier habitats with nematodes, tardigrades, rotifers, and protozoa in stream and lake hyporheic regions. To our knowledge, there are no reports of viruses from Antarctic invertebrates, although there is no reason to believe that such viruses do not occur because viruses infecting invertebrates have been reported from other ecosystems where the fauna is better characterized.

In contrast with the invertebrates, virological studies for marine birds and mammals that periodically visit the land surface of Antarctica are relatively numerous because of the emphasis placed on wildlife health and conservation in the face of pressure from humans. Viruses or viral antibodies for infectious bursal disease, avian influenza, and Newcastle disease have been detected in penguins (Barbosa and Jose Palacios 2009; Chang et al. 2009; Gauthier-Clerc et al. 2002; Miller et al. 2010; Morgan et al. 1981; Thomazelli et al. 2010; Wallensten et al. 2006) and skuas (Barbosa and Jose Palacios 2009; Miller et al. 2008). Reports of avian viruses in Antarctic ornithogenic soils are infrequent, even though these soils contain a large amount of accumulated guano, carcasses, and feathers and are probable reservoirs of avian viruses (Briggs et al. 2003). Weddell and crabeater seals with antibodies for canine and feline herpesvirus (Bengtson et al. 1991; Harder et al. 1991; Nelson et al. 2008; Tryland et al. 2012) and phocine distemper virus (Harder et al. 1991; Nelson et al. 2008) have been detected, but the occurrence of these viruses on land is unknown. Much of the concern about viruses in seabirds arises from the consequences of exposure to exotic viruses (Barbosa and Jose Palacios 2009; Grimaldi et al. 2011). The risks to penguins from infectious bursal disease virus and to seals from canine distemper virus (Cowan et al. 2011; Pearce and Wilson 2003) have contributed to restrictions on eggs being taken by humans to some parts of Antarctica as food and the removal of dogs from Antarctica. Exposure to humans is also a risk factor for Antarctic seabirds because of the concern about pandemic influenza (Kerry and Riddle 2009; Cowan et al. 2011).

5.3 Plant Viruses (Except Cyanobacteria and Algae)

Reports of viruses infecting plants in Antarctica are even more sparse than for animal viruses. There are two reports of viruses infecting higher plants in Antarctica: infection of *Deschampsia antarctica* (the only Antarctic monocotyledonous plant) and one report of viral moss infections. There are no reports of viruses infecting any other higher plant in Antarctica, the dicotyledonous *Colobanthus quitensis*, liverworts, or lichens. The report of Skotnicki et al. (2003) of the most southerly plant virus (Stilbocarpa mosaic bacilliform badnavirus infecting the sub-Antarctic herbaceous plant *Stilbocarpa polaris*) in 2003 on Macquarie Island has been more recently superseded by Parnikoza et al. (2007) and Polischuk et al. (2007) who reported *D. antarctica* viruses at sites around the Argentine Islands in the maritime Antarctic (Table 5.1). Polischuk et al. (2007) reported antigens in *D. antarctica* for cucumber green mottle mosaic virus, cucumber mosaic virus, and

Table 5.1 Reports of viruses from terrestrial Antarctica (excluding sea birds and mammals)

Location/Habitat	Host	Virus details (if any)	Reference
Continental Antarctica/dry valley soil	Soil bacteria	Unknown	Williamson et al. (2007)
	Staphylococcus pasteuri (bacterium)	Bacteriophage SpaA1 with phage MZTP02 in genome	Swanson et al. (2012)
	Bacillus cereus/ thuringiensis (bacteria)	Bacteriophage BceA1 with phage MZTP02 in genome	
Maritime Antarctica/ Argentine Islands	*Polytrichum* sp. (moss)	Tobamovirus Tobacco mosaic virus Cucumber green mottle mosaic virus	Polischuk et al. (2007)
	Barbilophozia sp. (moss)	Tobamovirus Tobacco mosaic virus Cucumber green mottle mosaic virus	
	Deschampsia antarctica (grass)	Cucumber green mottle mosaic virus Cucumber mosaic virus Tomato spotted wilt virus	
		Tobacco mosaic virus Cucumber green mottle mosaic virus Potato virus X Cucumber mosaic virus Alfalfa mosaic virus Tomato spotted wilt virus	Parnikoza et al. (2007)

tomato spotted wilt virus, all viruses that typically infect dicotyledonous plants. They also found antigens for tobamoviruses, tobacco mosaic virus, and cucumber green mottle mosaic virus in mosses of the genera *Polytrichum* and *Barbilophozia*, which they considered unusual because these viruses typically infect higher plants. It is possible that the apparently reduced host specificity reflects the more restricted range of host plants in Antarctica or greater susceptibility to virus infection under harsh environmental conditions. The absence of reports for viruses infecting liverworts or lichens cannot be regarded as no evidence for such infections in Antarctica; reports of viruses for liverworts or lichens are very rare for all ecosystems. Given that many herbivorous invertebrates, particularly insects and nematodes, are important vectors for the transmission of plant viruses in other ecosystems, it is probable that herbivorous invertebrates are also virus vectors in Antarctica. There are plenty of examples of invertebrate herbivory in the sub-Antarctic (e.g., Abraham et al. 2011; Bale et al. 2000; Hulle et al. 2003; Todd 1996), but as far as we are aware, there are no reports of invertebrates transmitting plant viruses in Antarctica.

5.4 Viruses in Soils

Reports of viruses in Antarctic soils are infrequent, but preliminary evidence indicates relative abundance by comparison with other groups of organisms. As part of a screening programme for viruses in soils, we extracted and concentrated viruses from soil samples from the dry valleys and used electron microscopy to examine morphology and abundance, and we also isolated bacteria from the soil and induced temperate phages from the bacterial cultures (Swanson et al. 2012). Viruses similar to known taxonomic groups of viruses were isolated using both approaches. Among the viruses directly extracted were spherical, tailed, and filamentous particles. The viruses isolated from the bacterial culture were mostly tailed viruses but also included some spherical and filamentous forms.

Tailed viruses Viruses with contractile tails which were morphologically similar to those belonging to the family *Myoviridae* were found but were often found damaged or separated into heads and tails. Using the bacterial culture approach, myoviruses (*Myoviridae*; viruses with long, rigid contractile tails) were associated with cultures of *Arthrobacter*, *Streptomyces*, *Staphylococcus,* and *Bacillus* species. Virus particles with spherical or elongated heads and long flexible non-contractile tails morphologically resembling bacteriophages of the family *Siphoviridae* (viruses with long, flexible non-contractile tails) were found (Fig. 5.1a, b) associated with *Arthrobacter*, *Streptomyces*, *Staphylococcus*, *Bacillus,* and *Aeromicrobium* species. Bacteriophages with icosahedral heads and short tails, morphologically similar to the *Podoviridae* (viruses with short, contractile tails), were isolated directly from the soils, but none were isolated from bacterial cultures.

Spherical viruses Spherical viruses of various sizes were isolated, and although identification of such virus particles by electron microscopy is difficult, the smallest spherical particles were similar in size (approximately 25 nm in diameter) to single-stranded RNA-containing bacteriophages of the family *Leviviridae*. Members of the *Leviviridae* family have been described associated with *Pseudomonas* species (Fauquet et al. 2005) which may give a clue to the host in the dry valley soil. Larger spherical particles with a diameter of approximately 40 nm (Fig. 5.1c) were similar in size to dsRNA-containing virus particles of the families *Partitiviridae*, C*hrysoviridae,* and *Totiviridae,* some members of which infect fungi (Fauquet et al. 2005). In addition, spherical particles (with a diameter of approximately 65 nm) with apical spikes were also observed. These particles resemble dsDNA-containing virions formed by members of the family *Tectiviridae,* which have been described associated with bacteria including *Bacillus* species (Fauquet et al. 2005). Virus particles morphologically similar to the *Tectiviridae* were also found associated with *Streptomyces* species (Fig. 5.1d).

Filamentous viruses Filamentous particles (Fig. 5.1e) were mostly about 7 nm in diameter and of variable lengths. Some resembled virus particles of the *Inovirus* genus with diameters of approximately 7 nm and between 700 and 2,000 nm in length. Viruses of this genus contain circular ssDNA within flexible filamentous virions and have been described associated with bacteria including *Pseudomonas*

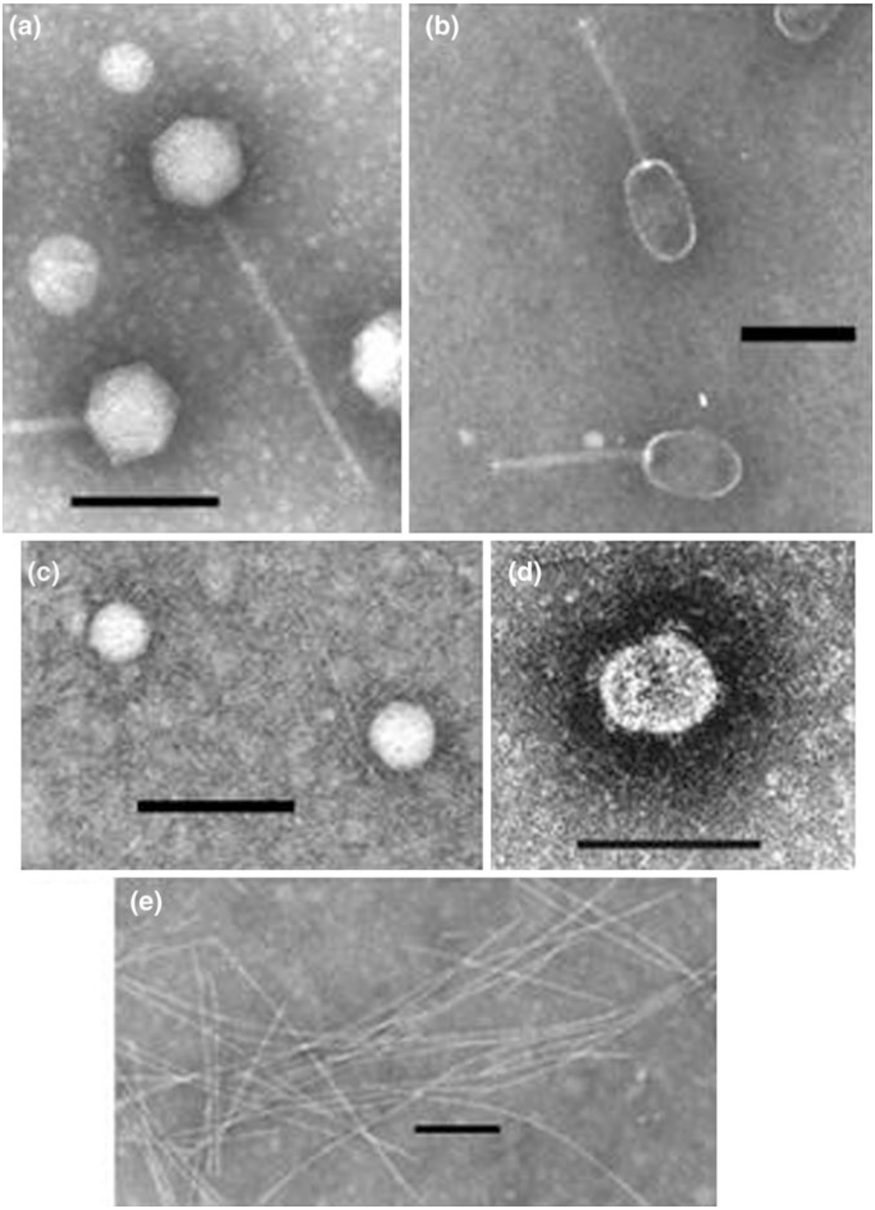

Fig. 5.1 Virus particles isolated from Antarctic soil. **a** Siphovirus particles isolated from a *Streptomyces* species. **b** Siphovirus particles isolated from a *Streptomyces* species. **c** Medium-sized spherical virus-like particles isolated directly from Antarctic soil. **d** Spiked spherical virus-like particle isolated directly from Antarctic soil. **e** Filamentous virus-like particles isolated directly from Antarctic soil

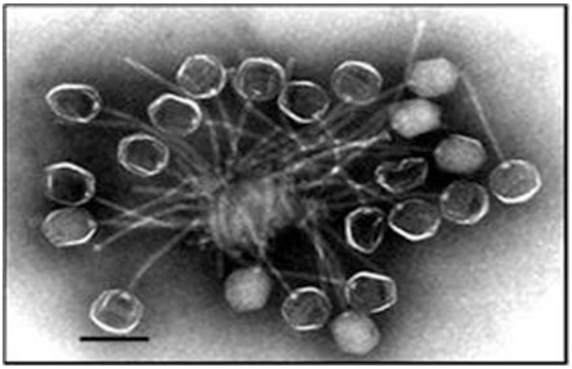

Fig. 5.2 Virus particles of SpaA1 from *Staphylococcus pastueri*

species (Ackermann 2005; Fauquet et al. 2005). Virus particles morphologically similar to *Inoviruses* were associated with *Staphylococcus* species in the dry valley soil.

In addition to our screening studies (above), there have been two more detailed reports of bacteriophages in Antarctic soils. Williamson et al. (2007) included soils from the dry valleys in an investigation of the bacterial lysogeny from inducible prophages. The viral abundances in these soils exceeded that of bacteria by more than 1,000-fold and were large in comparison with other soils investigated which were from temperate sites (Williamson et al. 2007), leading to speculation about whether the extreme cold and dry conditions of the dry valley contributed to preferential preservation of viruses in the soil (Williamson et al. 2007; Wommack 2010)—preservation in nature's freeze drier. The second record is the report of bacteriophages apparently with dual genomes—so-called Russian doll viruses—also from the dry valleys (Swanson et al. 2012; Fig. 5.2). In this work, the sequence of the bacteriophage MZTP02 was identified within the genome of bacteriophage SpaA1 from *Staphylococcus pastueri* and in the genome of another bacteriophage BceA1 from bacterium belonging to the *Bacillus thuringiensis/cereus* group. This may indicate that MZTP02 can be shuttled between genomes of other bacteriophages, leading to chimerical genomes, thereby providing a fast-track route for virus evolution and horizontal gene transfer. The occurrence of one phage genome entirely contained within the genome of another is a novel observation and leads to speculation about whether both genomes can be expressed and what regulatory control might exist over which genome is expressed. Currently, we have no knowledge of the regulatory mechanisms, but it is possible that the capability to switch between genomes may offer an evolutionary advantage in environments where bacterial hosts are relatively infrequent, as indicated by small microbial biomass (Barrett et al. 2006; Hopkins et al. 2006a, b) and the large phage-to-bacteria ratio (Williamson et al. 2007), or where the resource supply is sparse and intermittent (Hopkins et al. 2006a).

5.5 Relevance of Viruses in Lakes to Terrestrial Ecology

Lakes are an important driver of biological activity in terrestrial Antarctica. For example, the transfer of resources to the land surface as frozen and dried lacustrine detritus by the wind is a major spatial subsidy of organic carbon and other nutrients to the terrestrial community (Elberling et al. 2006; Hopkins et al. 2006a, b, 2008, 2009; Moorhead et al. 2003; Parker et al. 1982). This has two possible consequences. First, lakes may act as a source for the terrestrial virome, and second, regulation of the biological productivity and nutrient fluxes in lakes influences the resources available to the terrestrial community, especially in the absence of macroconsumers in the lakes as is the case in Antarctica. To our knowledge, there are no data on the transfer of viruses from lakes to terrestrial Antarctica, but given the abundance and ubiquity of viruses in Antarctic lakes (Pearce and Wilson 2003; Wilson et al. 2000), such transfers are highly likely. The fate of such virus particles is uncertain, but as discussed above, they may persist in some terrestrial environments. Over the past two decades, it has become clear that viruses are important regulators of planktonic, including cyanobacterial and algal, abundances and productivity (Kepner et al. 1998; Laybourn-Parry et al. 2001, 2002, 2007; Laybourn-Parry and Bayliss 1996; Pearce and Wilson 2003; Pearce and Laybourn-Parry 2012; Säwström et al. 2007a, b, 2008; Wilson et al. 2000; Yau et al. 2011), thereby exerting a degree of bottom-up control on terrestrial biological processes. It is notable that one of the few reports to date of a virophage, a sub-viral entity that parasitizes other phages by requiring coinfection of the algal host with another virus for replication while repressing replication of the second virus (Yau et al. 2011), are from an Antarctic source, perhaps indicating another adaptation to the relatively extreme Antarctic conditions. This virophage is similar to the recently discovered "Sputnik virus" which coinfects a protozoa host with a helper virus (La Scola et al. 2008).

5.6 Dispersal of Viruses

Antarctica is regarded as the most biologically isolated continent and the continent with the greatest degree of biological endemism (Adams et al. 2006; Green et al. 2011; Hogg et al. 2006; Novis and Smissen 2006). The route to Antarctica for the viruses of marine organisms and where human activity is involved are obvious, but the dispersal and transport routes to Antarctica for many other viruses with terrestrial hosts are less obvious. Although there are no reports specifically of airborne transport of viruses to Antarctica, there is ample evidence of transport of biological materials (e.g., fungal spores, pollen grains, bacteria, and fragments of lichens) to, within, and around Antarctica (Cowan et al. 2011; Harmata and Olech 1991; Marshall 1996, 1998; Morris et al. 2011; Pearce et al. 2009, 2010) to support the view that Antarctica is not virally isolated at least for those viruses that can become airborne.

5.7 Conclusions

Clearly, knowledge of the terrestrial virome of Antarctica is far from complete, and even where there is some information, it is fragmentary and frequently arising from incidental observations and opportunistic investigations. If the reports of viruses of seabirds and mammals are excluded on the basis that these hosts are only periodic visitors to the coast fringes of Antarctica, there are currently four published reports of viruses in terrestrial ecosystems in Antarctica (Table 5.1), only one of which (Swanson et al. 2012) is based on contemporary analysis using next-generation sequencing. The occurrence of apparently unusual observations, such as the "Russian doll" viruses (Swanson et al. 2012), virophage (Yau et al. 2011), and the large phage-to-bacteria ratios (Williamson et al. 2007) in Antarctica, may point to the novelty of the extreme environments, but with such a small number of studies so far conducted, further speculation is unwarranted. It is clear that understanding the terrestrial virome of Antarctica will require a substantial amount of research and may reveal novel viruses and novel aspects of viral ecology.

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Chapter 6
Microbiology of Eutrophic (Ornithogenic and Hydrocarbon-Contaminated) Soil

Jackie M. Aislabie, Phil M. Novis and Belinda Ferrari

Abstract Antarctic soils are typically low in carbon, nitrogen and phosphorus. Ornithogenic and hydrocarbon-contaminated soils, however, could be considered eutrophic. In this chapter, we review the microbial composition of ornithogenic and hydrocarbon-contaminated soils. Ornithogenic soils form in soils under bird nesting sites. These include those that form under penguin colonies of coastal soils and under bird nests in coastal soils and on nunataks. The soils currently occupied by birds have high levels of C, N and P and a low C:N ratio. The diversity and abundance of microbes in the soils depends on whether they are currently occupied by birds have been abandoned or are adjacent to the colony. Bacteria dominate occupied soils with Firmicutes reported to be prevalent, but in abandoned soils, Proteobacteria are dominant. Among the nematodes *Panagrolaimus* is most commonly reported from ornithogenic soils. Extensive areas of growth of visible photosynthetic microbes occupy soils adjacent to ornithogenic soils. *Prasiola* spp and *Phormidium* spp. are the dominant algae and cyanobacteria, respectively, that are reported. Most investigations of hydrocarbon-contaminated Antarctic soils have focused on heterotrophic bacteria, with a few reports of fungi. Hydrocarbon spills on soils typically occur next to research stations and result in an increase in soil C and a high C:N ratio. The result is a shift in microbial communities towards hydrocarbon-degrading species, predominantly from the Proteobacteria phylum. Among the hydrocarbon-degrading bacteria isolated from Antarctic soils are members of the genera *Pseudomonas*, *Sphingomonas* and *Rhodococcus*. These

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genera have been observed widely in contaminated temperate soils and have the capability to degrade hydrocarbons. Filamentous fungi from the Ascomycota phylum commonly isolated from contaminated soils include those from the *Cadophora, Trichoderma* and *Mortierella* genera, but their ability to degrade hydrocarbons is not always known. There is limited knowledge on the effect of hydrocarbons on Archaea, invertebrates or photosynthetic microbes in hydrocarbon-contaminated Antarctic soil. Our knowledge of eutrophic soils of Antarctica is sparse.

6.1 Introduction

Eutrophic soils are those high in nutrients. Although Antarctic soils are typically low in carbon, nitrogen and phosphorus, there are some exceptions (that is, ornithogenic and hydrocarbon-contaminated soils) that could be considered eutrophic. The term “ornithogenic soils” was first used by Syroechkovsky (1959) and later applied by Ugolini (1972) to soils which “consist of a layer of guano resting sharply on unconsolidated coarse sand” (Fig. 6.1). In Adélie penguin rookeries guano holds together stones, about 3–10 cm in diameter, that are used by the birds to build their nests on beach ridges, leading to the development of raised mounds that provide some protection from meltwater for the birds, their eggs and chicks (Hofstee et al. 2006). Ornithogenic soils may also derive from the guano of skuas and snow petrels that nest in coastal colonies or on nunataks.

In contrast to ornithogenic soils that occur naturally, hydrocarbon-contaminated soils have elevated levels of carbon, but not nitrogen or phosphorus, due to fuel spills resulting from human activities. Petroleum hydrocarbons are required for power generation, heating, and the operation of vehicles, aircraft and ships. Hence, accidental fuel spills on Antarctic soils occur mainly near settlements, including current and former scientific research stations and field camps where fuel is stored and aircraft and vehicles are refuelled (Aislabie et al. 2004).

6.2 Ornithogenic Soils

Ornithogenic soils form in coastal regions under penguin rookeries and on inland nunataks where birds nest. Compared with mineral soils, ornithogenic soils currently occupied by penguins are generally high in organic C, total nitrogen and phosphorus, and elevated electrical conductivity, while pH is variable and the C:N ratio is low (Table 6.1). Accumulated organic matter in soil from abandoned nest sites declines due to reduced inputs, decomposition and leaching (Zdanowski et al. 2005; Hofstee et al. 2006). Organic matter is brought to the rookery during summer when the penguins are ashore and is added to the soil as penguin guano,

Fig. 6.1 Photograph of Cape Hallett ornithogenic soil profile showing surface layers of stones held together by guano and overlying mineral soil (image supplied by M Balks, University of Waikato)

feathers, eggshells and bird remains. Guano contains uric acid, the primary nitrogenous waste product of birds, and undigested material such as chitin derived from krill, the almost exclusive food source of Adélie penguins. Although it breaks down rapidly in moist environments, uric acid is not readily degraded in arid soils (Ramsay and Stannard 1986).

Nitrogen in ornithogenic soils occurs as uric acid and ammonium with lesser quantities of nitrate (Speir and Cowling 1984). Ammonium and nitrate readily serve as nitrogen sources for microbial growth. Similarly, uric acid is degraded under aerobic and anaerobic conditions and can serve as both carbon and nitrogen sources. The detection of nitrate in ornithogenic soil may be due to in situ nitrification. Most phosphorus in ornithogenic soils occurs in organic and inorganic forms and has recently been shown to occur as matrix-bound phosphine, in soils of east Antarctica (Zhu et al. 2011). Both salts and ammonium contribute to the osmotic potential of ornithogenic soils with salts originating from guano and penguin nasal excretions as well as from seawater.

Table 6.1 Selected chemical and microbial properties of ornithogenic soils of Antarctica

Location	Soil depth (cm)	pH	Organic C (%)	Total N (%)	C:N ratio	Total P (%)	EC (mS/cm)	Total counts (g^{-1} dried weight)	Aerobic heterotrophs (g^{-1} dried weight)	Source
King George Island										
Stranger Point[a]	NR	NR	16.79	4.15	4	7.44	NR	NR	NR	Tatur et al. (1997)
Stranger Point[b]	NR	NR	7.07	0.98	7.3	9.20	NR	NR	NR	Tatur et al. (1997)
Ross Island										
Cape Bird[a]	0–5	6.5	22.6	17.0	1.3	2.6	25.3	3.0×10^9	NR	Aislabie et al. (2009)
	10–20	6.9	2.1	1.6	3.3	4.0	10.3	5×10^8	NR	
Cape Royds[b]	0–2	7.3	21.8	11.6	2.0	6.3	NR	NR	NR	Ugolini (1972)
	2–13	7.2	17.1	8.5	1.8	5.9	NR	NR	NR	
	13–28	7.1	0.4	0.4	1	0.5	NR	NR	NR	
Northern Victoria Land										
Cape Hallett[a]	0–10	7.7	11.7	4.7	2	3.6	15.4	6.8×10^9	1.1×10^8	Aislabie et al. (2009)
	10–25	8.0	9.4	4.2	2	5.1	13.5	1.8×10^9	6.1×10^6	
	40–50	8.3	0.2	0.2	1	0.5	1.5	2.6×10^8	2.4×10^3	
Cape Hallett[b]	0–5	5.6	4.3	0.9	5	3.6	1.2	1.6×10^9	1.1×10^8	Aislabie et al. (2009)
	30–60	5.9	0.1	0.04	3	0.5	0.1	4.3×10^7	1.4×10^5	
Soils surrounding snow petrel nests on nunataks in Dronning Maud Land										
Nest site	NR	NR	16.83	5.5	NR	5.3	NR	1.6×10^8	NR	Cocks et al. (1999)
1 m from nest	NR	NR	<0.3	<0.2	NR	<0.3	NR	5.0×10^7	NR	

[a] Soils occupied by penguins and [b] those abandoned. Where NR means not reported

6.2.1 Microbial Communities

Microbial biomass, respiration and nitrogen mineralization activity are typically higher in ornithogenic than in mineral soils (Roser et al. 1993; Tscherko et al. 2003; Barrett et al. 2006). In summer, midday soil respiration rates measured at Cape Hallett on an ornithogenic soil were an order of magnitude greater than that of mineral soils located in North and Southern Victoria Land (Barrett et al. 2006). Similarly, soils under the nests of snow petrels on a nunataks in Dronning Maud Land exhibited higher rates of respiration and than mineral soils away from the nests (Cocks et al. 1998). Orchard and Corderoy (1983) showed that decomposition rates in ornithogenic soils of Cape Bird were dependent on soil temperature and moisture. Barrett et al. (2006), however, reported that at Cape Hallett microbial biomass C, but not soil organic carbon or moisture contents, significantly influence rates of in situ soil respiration. Measurements of nitrous oxide and methane fluxes on ornithogenic soils were 1–2 orders of magnitude higher than those from moss-covered soils in maritime Antarctica (Sun et al. 2002). Bacteria dominated the soil microbiota of ornithogenic soils under active penguin colonies; few yeasts or fungal hyphae were revealed by microscopic examination (Roser et al. 1993). Total counts in ornithogenic soils ranged from 10^8 to 10^{11} g^{-1} of dry soil in surface soils (Ramsay and Stannard 1986; Roser et al. 1993; Bölter et al. 1997; Table 6.1) and the numbers of culturable bacteria varied from 10^5 to 10^8 g^{-1} (Ramsay and Stannard 1986; Pietr 1986). Highest numbers of heterotrophic culturable bacteria occur in surface organic layers and decrease with soil depth (Table 6.1). Among the culturable heterotrophs, bacteria that degrade proteins, uric acid and chitin were prevalent, as were endospore formers (Pietr 1986). Relatively high numbers of culturable uric acid degrading bacteria are present in ornithogenic soils, with 10^3–10^4 degraders g^{-1} dry soil at the surface declining to undetectable numbers in lower levels (Pietr 1986). In contrast to heterotrophs, the highest numbers of nitrifying bacteria have been detected in the soil layers deep in the soil profile (Pietr 1986). Investigations by Ayton et al. (2010) revealed that Archaea were either absent or below detection limits in ornithogenic soils. Although occupied soils within the penguin rookery are usually devoid of vegetation, abandoned soils or those on the margins of the rookery receiving nutrients in run-off may have diverse communities of photosynthetic organisms (Tatur et al. 1997).

6.2.1.1 Photosynthetic Microbes

Photosynthetic microbes are commonly encountered where ornithogenic soils predominate in Antarctica. They are more widely reported than heterotrophs, since they may be visible to the naked eye. Visible growths of most species result from the accumulation of individuals (such as numerous intertwined cyanobacterial trichomes), although in some (notably the green alga *Prasiola*), the individuals themselves can be macroscopic. Here, we treat *Prasiola* with microscopic genera, both for the sake of convention and for ecological commonality. The algae of lichen associations are not considered.

Definitions of both “ornithogenic” and “soil” have been relaxed for our purposes to include “bird-influenced”—substrates receiving variable inputs of guano and other ejecta from birds, as well as those having these inputs as their main origin—and terrestrial substrates where water can pond for some time. Algae are commonly encountered on dry soil in Antarctica, but the growth of these organisms occurs predominantly during or immediately after their inundation by water during melting events. Sampling sites have not always been described in detail, so the extent of bird influence and irrigation can be difficult to determine for some studies.

Unlike records of heterotrophs, the majority of photosynthetic microbes found to date in Antarctic ornithogenic soils were identified using microscopy and morphological features and represent sparser data from more sites. The organisms comprise four main groups: Cyanobacteria (“blue-green algae”, 29 genera, 42 subgeneric taxa), Chlorophyta + Charophyceae (“green algae”, 35 genera, 41 subgeneric taxa), Xanthophyceae (“yellow-green algae”, 9 genera, 11 subgeneric taxa) and Bacillariophyceae (“diatoms”, 26 genera, 43 subgeneric taxa). These totals omit unspecified identifications (e.g. *Chlorella* sp.) in the subgeneric tallies. The most commonly encountered taxa are listed in Table 6.2.

Prasiola spp. and the related *Prasiococcus calcarius* are the most widely encountered algae in ornithogenic habitats in Antarctica. *P. calcarius* is reported from at least 16 different regions of the Antarctic area considered in this chapter, and *Prasiola* from at least 25. Growths of these species are generally macroscopic and conspicuous, and *Prasiola* prefers well-irrigated soils, usually in association with dark mats of oscillatorialean cyanobacteria (Broady 1996). *Prasiola* from these habitats has usually been reported as *Prasiola crispa*. However, a recent study of Antarctic material in conjunction with the type material of this species showed that some specimens belong to a robustly separated lineage (now known as *Prasiola antarctica*; Moniz et al. 2012). Unfortunately, it is not currently possible to distinguish these lineages on the basis of morphology.

Drier ornithogenic soils contain diverse communities of microscopic chlorophytes (Broady 1996). Many of these require culturing for accurate identification and a paucity of morphological characters in the simpler forms means that identifications can still remain tentative in the absence of molecular data (which to date have seldom been obtained from Antarctic material). These include organisms referred to as species of *Chlorella* or *Chlorococcum*, and it is quite likely that these records conceal significant phylogenetic diversity.

Species of *Phormidium* are the most common cyanobacteria. These refer to filamentous forms with sheaths of varying thickness, and many forms have tapering ends and calyptrae. The genus is known to be polyphyletic, and new genera are gradually being erected to accommodate various clades (e.g. *Wilmottia*, Strunecký et al. 2011).

Table 6.2 List of microbial inhabitants of ornithogenic soils commonly reported from ornithogenic soils or those on the margins of the rookery receiving nutrients in run-off. Only the most common and dominant photosynthetic microbes are listed

Identity	Habitat	Location[a]	References
Photosynthetic microbes			
Cyanobacteria			
Aphanocapsa spp. *Leptolyngbya* spp. *Oscillatoria* spp. *Phormidium* spp.	Soils in penguin rookeries; soil associated with guano; mineral soils influenced by birds; soil in gull nesting areas; soil among moss cushions on penguin paths; rock surfaces near nesting birds; soil around petrel nests	AI, CP, DI, KGI, NI, TI, HP, GW, KI, VH, EP, WI, SI	Broady (1979a, b), (1986), (1989a), Heatwole et al. (1989), Ling and Seppelt (1998), Cavacini (2001), Mataloni and Tell (2002), Fermani et al. (2007), Smykla et al. (2007), González Garraza et al. (2011)
Diatoms			
Luticola spp. *Pinnularia* spp.	Soils in penguin rookeries; soil around gull nests; soil associated with guano	DI, CP, NI, SI, II, CR, VH	Hirano (1965), Broady (1979a, b), (1986), (1987), Mataloni and Tell (2002), Fermani et al. (2007), González Garraza et al. (2011)
Green algae			
Chlamydomonas spp. *Chlorella* spp. *Chlorococcum* spp. *Desmococcus* spp. *Prasiococcus calcarius* *Prasiola* spp. *Pseudococcomyxa simplex* *Stichococcus* sp.	Soil on penguin paths; soil associated with guano; soil in penguin rookeries; soil in gull nesting areas; bird remains; mineral soils influenced by birds; gravel fertilized by skuas; quartz stones embedded in soil near rookeries; petrel nesting areas; water-flushed ground enriched by birds	CP, TI, ArI, AI, NI, DI, KGI, VH, RI, SI, WI, BP, II, GW, EP, CW, CH, OI, LHB, EP, CB, CE, CC, CaB, MR	Rudolph (1963), Hirano (1965), Longton (1973), Hoshiai and Matsuda (1979), Broady (1979a, b), (1982), (1983), (1985), (1986), (1987), (1989a, b), Akiyama et al. (1986), Heatwole et al. (1989), Ling and Seppelt (1998), Cavacini (2001), Mataloni and Tell (2002), Fermani et al. (2007), Smykla et al. (2007), González Garraza et al. (2011)

(continued)

Table 6.2 (continued)

Identity	Habitat	Location[a]	References
Yellow-green algae			
Botrydiopsis spp.	Penguin walkways; soil surrounding penguin colonies; soil in gull nesting areas	VH, ArI, AI, NI, DI, CP, ChI, EP, OI	Broady (1979b), (1986), (1989a), Akiyama et al. (1986), Heatwole et al. (1989), Mataloni and Tell (2002), González Garraza et al. (2011)
Heterococcus spp.			
Xanthonema spp.			
Heterotrophic bacteria			
Firmicutes			
Unclass. *Bacillaceae*	Soil from nesting sites occupied by penguins	CH, CB	Aislabie et al. (2009)
Unclass. *Clostridiales*			
Sporosarcina			
Trichococcus			
Erysipelothrix			
Atopostipes			
Proteobacteria			
Alkanindiges	Soil from nesting sites occupied by penguins; soil from abandoned nesting sites	MI, CH	Bowman et al. (1996), Aislabie et al. (2009)
Dokdonella			
Lysobacter			
Psychrobacter			
Rhodanobacter			
Lysobacter			
Unclass. *Xanthamonadeaceae*			
Unclass. *Pseudomonadaceae*			
Unclass. *Rhizobiales*			
Bacteroidetes			
Unclass. *Flexibacteraceae*	Soil from nesting sites occupied by penguins; soil from abandoned nesting sites	CB, CH	Aislabie et al. (2009)
Unclass. *Saprospiraceae*			
Unclass. *Sphingobacteriales*			

(continued)

Table 6.2 (continued)

Identity	Habitat	Location[a]	References
Actinobacteria			
Arthrobacter	Soil from abandoned nesting sites within a penguin colony; soil from abandoned nesting sites within a penguin colony contaminated with oil	CH	Aislabie et al. (2009)
Mycobacterium			
Patulibacter			
Unclass. *Intrasporangiaceae*			
Unclass. *Microbacteriaceae*			
Deinococcus/Thermus			
Deinococcus	Soil from nesting sites occupied by penguins	CB	Aislabie et al. (2009)
Fungi			
Ascomycota			
Alternaria	Soil from within a penguin colony; soil impacted by nutrients from nearby penguin colony	WI, PL, CR, KGI	Fletcher et al. (1985), Arenz et al. (2006), Arenz and Blanchette (2009), (2011), Blanchette et al. (2010), Vaz et al. (2011)
Antarctomyces			
Cadophora spp.			
Candida spp.			
Cladosporium			
Debaryomyces			
Geomyces spp.			
Leuconeurospora			
Nadsonia			
Nectriaceae			
Onygenales			
Penicillium			
Phaeosphaeria			
Phoma			
Pseudeurotium			
Thelebolus			
Thielavia			
Theobolaceae			

(continued)

Table 6.2 (continued)

Identity	Habitat	Location[a]	References
Basidiomycota			
Bensingtonia	Soil from within a penguin colony; soil impacted by nutrients from nearby penguin colony	PL, CR, KGI	Arenz et al. (2006), Arenz and Blanchette (2009), (2011), Vaz et al. 2011
Bulleromyces			
Cryptococcus spp.			
Leucosporidiella			
Rhodotorula			
Zygomycota			
Mortierellaceae	Soil from within a penguin colony; soil impacted by nutrients from nearby penguin colony	CR, PL	Arenz et al. (2006), Arenz and Blanchette (2011)
Mortierella			
Nematodes			
Panagrolaimus	Occupied and abandoned penguin rookery soil	SI, As, CB, CH, BA, HA, S	Spaull (1973), Sinclair (2001), Porazinska et al. (2002), Barrett et al. (2006), Sohlenius and Boström (2008), (2009), Yeates et al. (2009)
Rhabditis	Penguin rookery soil; organic nest material of a sheath bill	SI	Spaull (1973), Maslen (1979)

[a] Key to locations: **Antarctic Peninsula**: AI Avian Island, ArI Argentine Island, As Astrolabe Island, CP Cierva Point, DI Deception Island, KGI King George Island, NI Neny Island, PL Port Lockroy, TI Torgerson Island. **Northern Victoria Land**: CH Cape Hallett, CW Cape Washington, EP Edmondson Point, GW Gondwana, HP Harrow Peaks, II Inexpressible Island, KI Kay Island. **Princess Elizabeth Land**: VH Vestfold Hills, RI Rauer Islands, MI Magnetic Island. **Marie Byrd Land**: EP Edward VII Peninsula. **Wilkes Land**: ChI Chapell Island, WI Windmill Islands, BP Bailey Peninsula. **Ross Island**: CaB Caughley Beach, CB Cape Bird, CE Cape Evans, CC Cape Crozier, CR Cape Royds. **Dronning Maud Land**: BA Basen nunatak, HA Haldorsentoppen nunatak, ST Steinnabben nunatak, OI Ongulkalven Island, LHB Lützow-Holm Bay. **Mac. Robertson Land**: MR Mawson Rock, WI Welch Island. **Other**: SI Signy Island

The most common diatom species found are those of *Luticola* and *Pinnularia*. Morphological identifications of diatoms are generally more reliable than those of "soft algae", being based on features of silica frustules that can be readily preserved. The diatom flora of Antarctica is depauperate in species compared with floras of other regions, with approximately 40 species in all terrestrial Antarctic habitats (Broady 1996). Since 43 subgeneric diatom taxa are found in the literature from nominally ornithogenic soils, it follows that the majority of the species known from Antarctica can be found in enriched sites.

Does the ornithogenic habitat select a particular flora? The answer is not clear-cut. It is known that substances found in ornithogenic soils, such as acrylic and oxalic acids, can prevent the growth of algae (e.g. Kol 1970; Akiyama et al. 1986). Irrigated soil in the immediate vicinity of penguin colonies often supports *Prasiola*, *Prasiococcus*, oscillatorialean mats, and the diatom *Luticola*. However, the eutrophication of these soils occurs on a continuum, and the likelihood of encountering more generalist algal species increases as the influence of birds wanes. Many species recorded from soils influenced by birds have also been found elsewhere, often as part of the same survey, such as *Botrydiopsis constricta* and *Cyanothece major* from the Antarctic Peninsula and South Georgia (Broady 1979b), *Phormidium autumnale* from numerous sites (e.g. Broady 1979a, b, 1986, 1989a; Fermani et al. 2007; González Garraza et al. 2011), *Tribonema vulgare* from Cierva Point, Antarctic Pensinsula (Mataloni and Tell 2002), *Mayamaea atomus* from the Vestfold Hills (Broady 1986), and *Desmococcus olivaceus* from many sites including the Windmill Islands, Wilkes Land (Ling and Seppelt 1998). All these species are also found outside Antarctica, in non-ornithogenic soils and other habitats.

6.2.1.2 Heterotrophic Bacteria

The bacterial composition of ornithogenic soils from Cape Hallett and Cape Bird has been determined using 16S rRNA gene clone libraries prepared from total community DNA (Aislabie et al. 2009). The clones numerically dominating the respective samples were sequenced and revealed to be taxonomically affiliated with the phyla Firmicutes, Proteobacteria, Actinobacteria, Bacteroidetes and Deinococcus-Thermus (Fig. 6.2). The clones were taxonomically affiliated with heterotrophic bacteria that grow under aerobic or anaerobic conditions. The composition of the soils was dependent on the influence of penguins. For those sites currently occupied, Firmicutes were prevalent, whereas Gammaproteobacteria, Actinobacteria and Bacteroidetes dominated abandoned soil. Investigation of ornithogenic soil from Signy Island using DGGE revealed a dominance of Bacteroidetes (Chong et al. 2009a). The environmental variables that best explain differences in bacterial community composition structure include nutrients (C, N and P) and salinity (measured as electrical conductivity) (Aislabie et al. 2009).

Most of the clones (>60 %) retrieved from soil occupied by penguins from Cape Hallett and Cape Bird belonged to the Firmicutes. Many of the Firmicutes

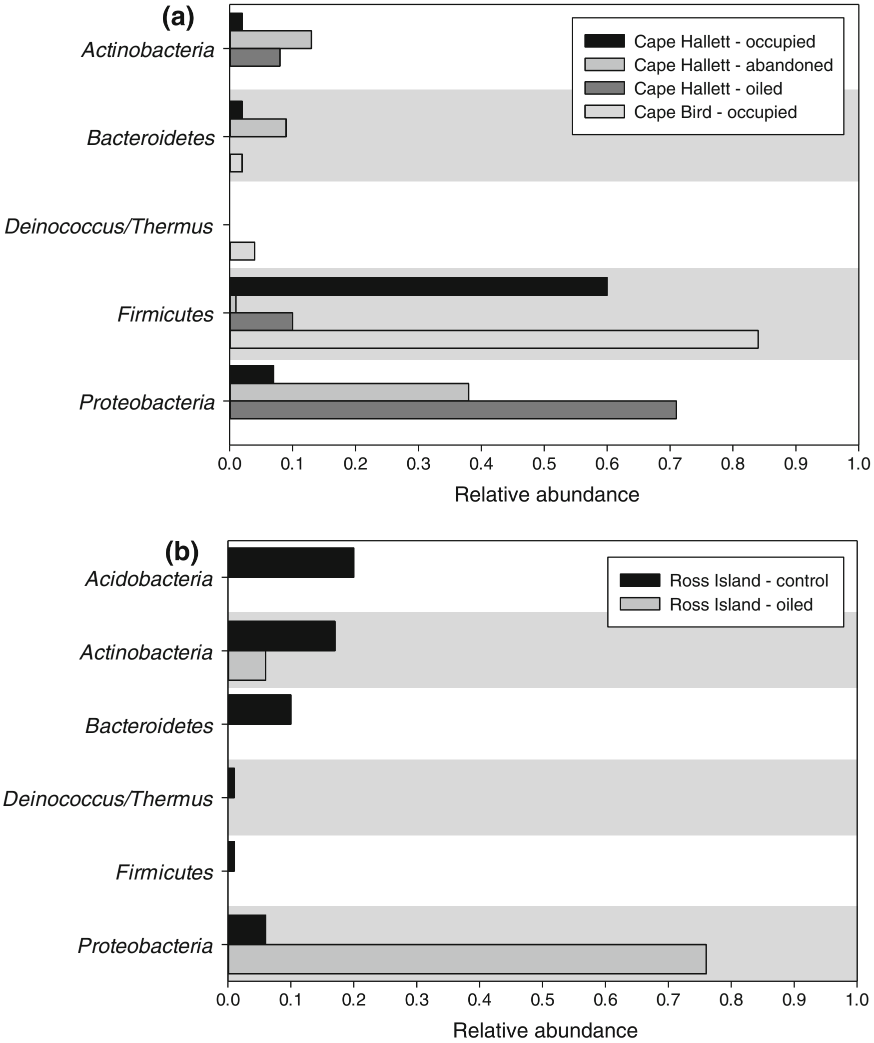

Fig. 6.2 Histograms depicting the relative abundance of the major bacterial phyla detected in **a** Cape Hallett ornithogenic soils (occupied, abandoned and hydrocarbon-contaminated), and **b** Ross island mineral soil (hydrocarbon-contaminated and control). Clones present at low abundance (and hence not sequenced) are excluded from the histograms

were most closely related to heterotrophic endospore-forming bacteria (Aislabie et al. 2009). As endospore production confers an ability to survive inhospitable conditions, it may aid the ability of bacteria to colonize and survive in soils occupied by penguins. The most common phylotype detected in the Cape Bird and Cape Hallett soil belonged to the Bacillaceae and was most closely affiliated with a group of moderately halotolerant bacilli including the genera *Oceanobacillus,* *Paucisalibacillus*, *Salinibacillus* and *Virgibacillus.* The closest cultured relative of the clones was *Oceanobacillus profundus,* a salt- and alkali-tolerant bacterium (Kim et al. 2007). Other putatively halotolerant bacteria detected in the soil belonged to *Sporosarcina.* The second most common Firmicutes phylotype detected in Cape Hallett soil belonged to the order Clostridiales and was distantly related to *Clostridium acidurici* and *Clostridium purinilyticum.* These bacteria metabolize purines, uric acid derivatives and pyrimidines for growth anaerobically, implying that microbes belonging to this phylotype may degrade uric acid under anaerobic conditions in penguin-colonized soils of Cape Hallett. Firmicutes were also prevalent in Adélie penguin guano (Banks et al. 2009); however, they were not closely related to those detected in ornithogenic soils. Banks et al. (2009) detected Fimicutes related to *Mycoplasma* spp., *Peptostreptococcus* spp and *Guggenheimella bovis* in the faecal flora of Adélie penguins. Attempts to culture Firmicutes representative of the dominant phylotypes from soil have so far been unsuccessful.

Gammaproteobacteria were prevalent in ornithogenic soil from Cape Hallett but not detected in soil from Cape Bird and were more common in abandoned soil than occupied soil. In occupied soil, the Gammaproteobacteria belonged to the genus *Psychrobacter.* Novel strains of *Psychrobacter* isolated from ornithogenic soils of East Antarctica degraded uric acid and were halotolerant (Bowman et al. 1996). *Psychrobacter* spp. have also been isolated from guano of an Adélie penguin (Zdanowski et al. 2004). In contrast to occupied soil, the gammaproteobacterial phylotypes detected in the abandoned soil were more diverse and typically assigned to the family Xanthomonadaceae. The closest relatives of the gammaproteobacterial phylotypes were uncultured bacterial clones, some of which were detected in Antarctic lake sediment receiving penguin droppings. The closest relatives of the Xanthamonadaceae include bacteria belonging to the genera *Rhodanobacter* and *Dokdonella.* Some *Rhodanobacter* species use amino acids rather than sugars for growth, produce proteases, and may grow under nitrate-reducing conditions (Lee et al. 2007). Members of the Xanthamonadaceae likely contribute to organic matter decomposition in situ.

The few clones detected in Cape Hallett occupied soil and assigned to Actinobacteria were not affiliated with known families, indicating they are novel. In contrast, the actinobacterial clones from the abandoned soil were more diverse; a few belonged to *Patulibacter* or *Mycobacterium* but others could not be assigned to known genera. Actinobacteria isolated from soils are saprophytes, recognized for their ability to metabolize a wide range of substrates including amino acids and sugars. Although Bacteroidetes were minor constituents of Cape Hallett and Cape Bird soil, they were dominant in ornithogenic soil from Casey Station in East Antarctica (Chong et al. 2009b) and Signy Island (Chong et al. 2009a). Closest relatives of the Bacteroidetes detected in the soil included clones detected in Antarctic lake sediment receiving penguin guano. Bacteroidetes were detected in Adélie penguin guano (Banks et al. 2009), prominently during early stages of guano decomposition (Zdanowski et al. 2004) and have been implicated in degradation of chitin in Antarctic sediments receiving penguin guano (Xiao et al.

2005). A few clones from Cape Bird soils were assigned to the genera *Deinococcus* which falls within the extremotolerant phylum Deinococcus/Thermus.

6.2.2 Fungi

Investigations of fungi in Antarctic soils have generally involved cultivation on agar plates and then identification using morphology and, increasingly, molecular tools (Arenz and Blanchette 2009). As for Antarctic soils, in general, it appears that most fungi in ornithogenic soils belong to the phylum Ascomycota with fewer Basidiomycota and Zygomycota (Fletcher et al. 1985; Arenz et al. 2006; Arenz and Blanchette 2009; Blanchette et al. 2010; Table 6.2). Common among the Ascomycota were *Geomyces* and *Cadophora* species, which have been isolated from soils associated with penguin rookeries of Port Lockery and/or Cape Royds (Arenz et al. 2006; Arenz and Blanchette 2009; Blanchette et al. 2010). *Geomyces* species include the fungus formerly known as *Chryosoporium pannorum.* This fungus is cellulolytic and keratinolytic, grows well at low temperatures, and has also been isolated from feathers, nests and mud in Elephant seal wallows on Signy Island (Pugh and Allsopp 1982). Blanchette et al. (2010) suggested that high-nutrient concentrations may be promoting growth and activity of *Cadophora* species isolated from soil at Cape Royds. Some of the fungal isolates from ornithogenic soils such as the cosmopolitan *Thelebolus* (in particular *Tylopilus microsporus*) are reported to be psychrophilic and coprophilic and have been isolated from skua dung and feathers (de Hoog et al. 2005). Thermophilic fungi such as *Aspergillus fumigatus* and *Chaetomium gracile* have been isolated from soils and guano, but it is not known if they are active in soil (Wicklow 1968; Ellis 1980).

Numbers of culturable yeasts detected in ornithogenic soils of King George Island ranged from 10^2 to 10^3 g^{-1} of soil (Vaz et al. 2011). Eleven isolates were identified as belonging to the genera *Bensingtonia*, *Candida*, *Cryptococcus*, *Leuconeurospora*, *Leucosporidiella* and *Nadsonia*, and none were unique to ornithogenic soils. *Cryptococcus* and *Candida* have also been isolated from soils within a penguin rookery at Port Lockery and/or Cape Royds (Arenz et al. 2006; Arenz and Blanchette 2009; Blanchette et al. 2010). Some of the yeast are reported to be cold-tolerant, including *Cryptococcus* and *Nadsonia*, and are thought to be endemic in Antarctic and sub-Antarctic soils (Ferrari et al. 2011).

6.2.2.1 Invertebrate Communities

Ornithogenic soils that have formed under penguin colonies or near bird nests have been examined for nematodes, and sometimes for rotifers and tardigrades. These investigations have revealed that the bacterial-feeding nematode *Panagrolaimus* is most commonly associated with ornithogenic soils with *P. davidii* (Sinclair 2001; Porazinska et al. 2002; Barrett et al. 2006; Yeates et al. 2009) reported from Ross island and Cape Bird and *Peromyscus maniculatus* from Dronning Maud Land (Sohlenius and Boström 2008, 2009). *Panagrolaimus* along with *Rhabditis* sp. (originally identified as *Caenorhabditis* sp.) have been reported to dominate ornithogenic soil samples from maritime Antarctica (Spaull 1973; Maslen 1979; Table 6.2). Numbers differ between sites and with sampling time; and distribution may be patchy, with less than 50 % of soil samples examined from penguin rookeries of Ross Island reported to contain invertebrates (Porazinska et al. 2002). Nematodes and rotifers may occur in the same samples, whereas tardigrades are rare (Porazinska et al. 2002; Sohlenius and Boström 2008). Sohlenius and Boström (2008) speculated that the high abundances of nematodes detected in soils near snow petrel nests on nunataks of Dronning Maud Land were due to a high supply of food resources and an absence of predation. Analysis of the class size distribution and the occurrence of adults in soils from Cape Hallett over a 2-month sampling period, over spring and summer, indicated an annual life cycle for *Panagrolaimus* (Yeates et al. 2009). Nematodes are more abundant and diverse in soils on the rookery margins receiving nutrients; for example, *Panagrolaimus*, *Plectus* and *Eudorylaimus* have been detected in soils adjacent to the rookery at Cape Hallett (Barrett et al. 2006). Contrary to the expectations of Porazinska et al. (2002), higher-nutrient, organic matter and moisture levels did not result in more abundant and diverse invertebrate communities in ornithogenic soils. Hence, these authors proposed that high soil salinity due to excess nutrients may limit invertebrate presence within active rookeries.

6.3 Hydrocarbon-Contaminated Soils

Total petroleum hydrocarbon (TPH) analysis of soil samples from near fuel storage tanks, fuelling stations, and machine shops confirmed the presence of hydrocarbon contamination in Antarctic soils (Aislabie et al. 2004). Chemical characterization of the hydrocarbon contaminants revealed that *n*-alkanes predominate with lesser concentrations of aromatic compounds. The petroleum contaminants of greatest concern are polycyclic aromatic hydrocarbons (PAHs) due to their potential toxicity and environmental persistence. In Antarctica, methylnaphthalenes account for the majority of the PAH contaminants (Aislabie et al. 2004; Kim et al. 2006). This reflects the prevalence of naphthalene and methylnaphthalene, and low concentrations of larger molecular weight PAHs in aviation fuel such as JP-8 jet fuel, the major type of fuel used and hence spilled. JP-8 has about 80 % *n*-alkanes in the range of C_6-C_{18}, with a maximum at C_{12}, and 18 % aromatics with <0.5 % PAHs having three or more rings. At some spill sites, residual hydrocarbons were detected predominantly as an unresolved complex mixture. This is indicative of a number of sources including lubricating oils, motor oils, or severely biodegraded or weathered oils. When spilled on Antarctic soils, possible mechanisms for loss of hydrocarbons include dispersion, evaporation and biodegradation (Aislabie et al. 2004).

6.3.1 *Microbial Communities*

Studies on the impacts of hydrocarbon spills on Antarctic soil microbes were originally initiated as part of the environmental monitoring programme for the Dry Valley Drilling Project. More recent investigations derive from interest in the potential application of bioremediation for clean-up of hydrocarbon-contaminated soils. These investigations have focused on heterotrophic bacteria and fungi.

Fuel spills on Antarctic soils can result in enrichment of hydrocarbon-degrading microbes within the indigenous microbial community (Aislabie et al. 2004). Hydrocarbon-degraders have been cultivated at levels $>10^5$ g^{-1} from contaminated soils, whereas numbers of hydrocarbon-degraders are often low or below detection limits in pristine soils. The detection of hydrocarbon mineralization activity in Antarctic mineral (Aislabie et al. 1998, 2012; Ferguson et al. 2003) and ornithogenic soil (Aislabie et al. 2009), albeit in the laboratory, indicates that the hydrocarbon-degraders can be active in situ, conditions permitting. Fuel spillage on mineral soil increases the soil C/N ratios and can deplete available nitrogen and phosphorus, which are assimilated during biodegradation (Aislabie et al. 2012).

There has been little consideration of the impacts of hydrocarbons on Archaea, photosynthetic microbes and invertebrates in Antarctic soils (Kerry 1993; Ayton 2010). Crenarchaea and Euryarchaea (related to *Methanosarcina*) were detected in hydrocarbon-contaminated soils from Scott Base and Marble Point, respectively, and numbers were tenfold lower than bacteria (Ayton 2009). Estimates of amoebae were higher in hydrocarbon-contaminated soil treated with nutrients than uncontaminated and contaminated control soils, indicating that they may be capable of growth in situ on oil-degrading bacteria (Kerry 1993).

6.3.1.1 Heterotrophic Bacteria

Both culture-dependent and culture-independent methods have been employed to determine the impacts of hydrocarbon contamination on the diversity of bacterial communities in Antarctic soils.

16S rRNA gene clone libraries were prepared from total community DNA extracted from two soil depths in hydrocarbon-contaminated and control mineral soil near Scott Base on Ross Island (Saul et al. 2005) and ornithogenic soil from Cape Hallett (Aislabie et al. 2009). Clones numerically dominating the respective samples were sequenced. In the mineral soil, members of the phlya Acidobacteria, Bacteroidetes, Deinococcus/Thermus, Firmicutes and Candidate TM7 occurred exclusively in the control soils, whereas the contaminated soils were dominated by Proteobacteria (Fig. 6.2b). Similarly, Proteobacteria were dominant in oiled soil from King George Island (Foong et al. 2010). Conversely, both control (abandoned) and contaminated ornithogenic soils were dominated by Proteobacteria (Fig. 6.2a) (Aislabie et al. 2009). Spillage of oil on mineral soil can lead to a decrease in overall soil bacterial diversity (Saul et al. 2005; Chong et al. 2009b;

Foong et al. 2010), whereas for ornithogenic soil, an increase in bacterial diversity was detected in the surface organic soil layer but a decrease in the subsurface mineral layer (Aislabie et al. 2009).

Culturing bacteria from hydrocarbon-contaminated soils has focused on the isolation of hydrocarbon-degraders (Aislabie et al. 2006). The isolated bacteria have been assigned to the bacterial phyla Proteobacteria or Actinobacteria. Hydrocarbon-degrading bacteria from Antarctic soils are commonly psychrotolerant rather than psychrophilic, grow at low temperatures (<10 °C) but have an optimum growth temperature >15 °C. Some of the isolates produce biosurfactants to aid hydrocarbon degradation (Vasileva-Tonkova and Gesheva 2007).

Proteobacteria-dominating hydrocarbon-contaminated mineral soils of Ross Island were assigned to Alpha-, Beta- and Gammaproteobacteria, specifically members of the genera *Sphingomonas*, *Sphingobium* (formerly included in *Sphingomonas*), *Pseudomonas* or *Variovorax* (Saul et al. 2005). In ornithogenic soil, Gammaproteobacteria dominated the control (abandoned) and contaminated soil (Aislabie et al. 2009), with those dominating the control soil most closely related to *Rhodanobacter* or *Dokdonella*, and those in the oiled soils related to *Alkanindiges* and *Psychrobacter*. Members of the *Sphingomonas*, *Sphingobium* and *Pseudomonas* genera are often implicated in aromatic hydrocarbon degradation. *Sphingobium* sp. Ant 17, for example, degrades numerous compounds in the aromatic fraction of crude oil, jet fuel and diesel fuel (Baraniecki et al. 2002) and utilizes many aromatic compounds for growth, including *m*-xylene, naphthalene and its methyl derivatives, and fluorene and phenanthrene. Cold-tolerant hydrocarbon-degrading *Pseudomonas* strains Ant 9 and ST41 cluster together by 16S rRNA gene analysis with *Pseudomonas syringae* (Aislabie et al. 2006), whereas others cluster with *Pseudomonas fluorescens* or *Pseudomonas stutzeri*. *Sphingobium* isolates Ant 17 and 44/02 clustered with *Sphingomonas chlorophenolica* and are related to aromatic-degrading *Sphingobium* spp. from globally distributed sources (Aislabie et al. 2006). *Sphingomonas* sp. Ant 20 has been assigned to the species *Sphingomonas aerolata.* Ma et al. (2006) found that catabolic genes amplified from several aromatic-degrading psychrotolerant *Pseudomonas* isolates from contaminated Antarctic soils are closely matched to those described in mesophilic bacteria.

Some Proteobacteria such as *Pseudomonas* spp. 5A and 5B fix nitrogen in addition to utilizing mono-aromatic hydrocarbons or hexane, respectively (Eckford et al. 2002), whereas others degrade hexadecane under denitrifying conditions (Powell et al. 2006). A hydrocarbon-degrading bacterium isolated from contaminated ornithogenic soil from Cape Hallett was identified as *Alkanindiges* CH71i (Aislabie et al. 2009). This bacterium clustered with the type strain *Alkanindiges illinoisensis* and a single phylotype detected in the subsurface mineral layer of a contaminated ornithogenic soil pit at Cape Hallett. Growth of CH71i on R2A agar, like the type strain, was greatly enhanced in the presence of *n*-alkanes (Bogan et al. 2003). *Pantoea* sp. Strain A-13, isolated from ornithogenic soils, produced emulsifying agents when grown on *n*-paraffins or kerosene as sole source of carbon and energy (Vasileva-Tonkova and Gesheva 2007).

Members of the Actinobacteria were found in both oiled and control soils (Fig. 6.2a). However, whereas *Rubrobacter* were most prevalent in the control soil from Scott Base, *Rhodococcus* spp. were prevalent in the oiled soil (Saul et al. 2005). Alkane-degraders belonging to *Rhodococcus* are frequently isolated from Antarctic soil (Aislabie et al. 2006). *Rhodococcus* spp. strains 7/1, 5/1 and 5/14 grew on a range of alkanes from hexane (C_6) through at least eicosane (C_{20}) and the isoprenoid compound pristane (2, 6, 10, 14-tetramethyl-pentadecane) (Bej et al. 2000). Phylogenetic analysis of 16S rRNA genes from the *Rhodococcus* isolates indicates that they group with *Rhodococcus erythropolis* or *Rhodococcus fascians* and other *Rhodococcus* isolates from cold soils such as *Rhodococcus* Q15 (Aislabie et al. 2006). Although other *Rhodococcus* isolates are reported to degrade aromatic compounds, the known isolates from Antarctica appear to degrade alkanes exclusively (Aislabie et al. 2006). Alkane-degrading *Actinobacteria* isolated from ornithogenic Antarctic soil, including isolates identified as *Rhodococcus*, *Gordonia* or an unclassified *Corynebacterineae*, mineralized hexadecane when grown with either ammonium nitrate or uric acid as sole nitrogen source (Aislabie et al. 2008). An investigation of functional genes encoding enzymes for alkane degradation led Whyte et al. (2002) to propose that *Rhodococcus* is the predominant alkane-degrader in both control and hydrocarbon-contaminated Antarctic soils.

6.3.1.2 Fungi

Filamentous fungi and to a lesser extent yeasts from the Ascomycota phylum are commonly associated with petroleum contamination in Antarctic soils (Aislabie et al. 2001; Hughes et al. 2007). However, there is limited understanding of those species that are not just tolerant to, but are capable of degrading hydrocarbons. Antarctic fungi tolerant to aliphatic and/or aromatic hydrocarbons include widely distributed species from within the *Mortierella*, *Trichoderma*, *Mollisia*, *Phoma* and *Penicillium* genera (Hughes et al. 2007). High numbers of *Cadophora* (formerly *Phialaphora*) and *Hormoconis resinae,* along with significant increases in total counts, have been observed in several contaminated Antarctic soils compared with pristine soils that were dominated by *Geomyces*, *Phoma* and *Geotrichum* (Kerry 1990; Aislabie et al. 2001; Arenz et al. 2006). This shift in species composition after hydrocarbon contamination has been observed widely in both laboratory and microcosm studies and is a phenomenon that occurs quite quickly in response to contamination with hydrocarbons (Ferrari et al. 2011). Antarctic species capable of degrading aliphatic hydrocarbons include *Mortierella* and *Trichoderma* genera (Hughes et al. 2007). Knowledge is limited to the capability of both Antarctic and temperate fungi to degrade hydrocarbons. Given the fact that fungi play a major role in soil processes such as biodegradation, much more work is necessary to characterize the hydrocarbon-degrading potential of dominant species before we can completely understand the importance of fungi within microbial communities in hydrocarbon-contaminated Antarctic soils.

6.4 Conclusions

Our knowledge of the microbial composition of Antarctic eutrophic soils is limited. It appears that the microbial community of eutrophic soils may be more abundant but less diverse than that of mineral Antarctic soils. Certainly, bacteria in ornithogenic soils occupied by penguins were more numerous than in mineral soils, but subsequent investigations revealed that the bacterial and nematode communities were less diverse. Three bacterial phyla were detected in occupied soils from Cape Hallett compared with nine in mineral soils from Ross Island. This is likely due to the higher osmotic potential of soils occupied by penguins, compared with that of mineral soils. Similarly, numbers of culturable bacteria in hydrocarbon-contaminated soils may be higher, but the in situ bacterial community was less diverse than pristine soil and was dominated by Proteobacteria. This is likely due to selection of hydrocarbon-degrading bacteria but may also be due to selective toxicity of the fuel to members of the soil microbial community. In contrast to ornithogenic soils occupied by penguins, those that are abandoned or adjacent likely have a more diverse microbial community. Clearly such soils exhibit extensive growth of photosynthetic organisms and have a more abundant and diverse invertebrate community.

Comparison of eutrophic soils with mineral soils indicates that the microbial communities differ; however, the response of the soils to shifts in nutrient concentrations is unknown. Key questions regarding microbial community dynamics include how quickly the community responds to spills of hydrocarbons (increase in carbon and decline in C:N ratio) or attempts to remediate the soil (by augmentation with N and P). Similarly, how long is needed for the microbial population to shift following abandonment of the soils by penguins and resulting declines in C, N, P and salinity? The application of new-generation sequencing technologies and microarrays to investigations of eutrophic soils will greatly increase our knowledge of the composition of eutrophic soils and their response to shifts in nutrient concentrations.

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Chapter 7
Fell-Field Soil Microbiology

Etienne Yergeau

Abstract Only 0.33 % of the Antarctic land surface area is free of ice, with much of this area representing fell-field environments. Antarctic fell-fields are a type of tundra ecosystem that are generally nutrient-limited (especially N) and have a sparse cover of vegetation that is dominated by lichen or bryophytes, although dense vegetative cover and even vascular plants can be present in moister fell-field habitats. Environmental conditions are generally unfavourable in fell-field Antarctic environments, but these soils are spectacular in terms of the diversity of conditions that they offer for microbial life. This is reflected in the variety of microbial taxa and functions that can be found in these environments. Several factors were identified as having strong influences on the microbial communities inhabiting Antarctic fell-field soils, including water, temperature, plants, birds and pH. This chapter reviews microbiological studies that have been carried out in Antarctic fell-field soils.

7.1 The Fell-Field Environment

Only 0.33 % of the Antarctic land surface area is free of ice (Fox et al. 1994), with much of this area represented by fell-field environments (Block et al. 2009). Antarctic fell-fields are a type of tundra ecosystem, which have been shaped by rock and glacial till, and are subjected to the effects of cryoturbation and permafrost. Antarctic fell-fields are generally nutrient-limited (especially N), and most fell-field soils have a sparse cover of vegetation that is dominated by lichens or bryophytes. However, dense vegetative cover and even vascular plants can be present in moister habitats (Block et al. 2009). Environmental conditions are

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generally unfavorable in Antarctic fell-field environments, with a low thermal capacity in the substratum, frequent freeze–thaw and wet–dry cycles, low and transient precipitation, reduced humidity, rapid drainage, and limited organic nutrients (Wynn 1990; Convey 1996; Block et al. 2009). These generally adverse conditions support relatively simple ecosystems with a noted reduction in the complexity of food webs. (Wall and Virginia 1999). Annelids, mollusks, winged insects, and mammals are effectively absent from these systems, and only two native vascular plant species have been found to inhabit Antarctic terrestrial environments (Davis 1981). Consequently, most of these soil environments are devoid of vascular plant root systems and larger animals, which would normally cause bioturbation. Although some complex trophic interactions have been identified in terrestrial Antarctic environments (Newsham et al. 2004), the relatively simplified food web structure of Antarctic soils provides a model system in which to disentangle the drivers and consequences of microbial activities in the fell-field soil system.

Two main categories of Antarctic fell-field soils have been identified based on cluster analysis of a range of abiotic and biotic factors: (1) nutrient-poor, dry, bare mineral soils and (2) moist, relatively nutrient-rich, vegetated soils (Bölter 1990). Recent warming trends across the Antarctic are thought to be contributing to the expansion of vegetated areas, as well as to changes in macrophyte distribution patterns throughout this region (Fowbert and Smith 1994; Smith 1994b; Convey 2003). This chapter reviews microbiological studies that have been carried out in Antarctic fell-field soils. For the purpose of this review, I will use the fell-field definition of Block et al. (2009) and exclude ornithogenic soils that are covered in Chap. 6.

Bacteria and fungi have a large influence in fell-field soils, as they were reported to be responsible for 81–89 % of heterotrophic respiration in Signy Island fell-field soils, while 10–19 % of soil respiration was due to protozoan activity and 0.42–0.48 % of soil respiration was due to rotifers, tardigrades, nematodes, acari, and collembola (Davis 1981).

7.2 Bacteria

7.2.1 *Influencing Factors*

Different bacterial community parameters (abundance, structure, activity, and diversity) have been linked to a range of environmental factors in southern polar fell-field environments. The availability of water appears to be the major factor dictating cyanobacterial distribution (Christie 1987; Bölter et al. 1997; Smith et al. 2006), bacterial abundance (Christie 1987; Tearle 1987), activity (Christie 1987; Bölter 1992), and diversity (Aislabie et al. 2006). Other evidence suggests that bacterial abundance and activity are controlled by the availability of organic matter and the supply of soluble carbohydrates and amino acids (Christie 1987;

Bölter 1992; Vishniac 1993) or the presence of vegetation (Bölter 1995; Bölter et al. 1997; Yergeau et al. 2007a). In contrast to what is generally recognized for Arctic habitats (Jonasson et al. 1999), some Antarctic studies have reported that microbial activity was not primarily limited by the availability of N and P (Christie 1987; Bölter 1992). One study suggested that the structure of soil-borne communities was mostly coupled to factors related to latitude (mean temperature, pH, C:N ratio, etc.), whereas abundance data were mostly influenced by plant-related factors (organic C, soil humidity, total N, etc.) (Yergeau et al. 2007a). Recent studies on Signy Island also identified pH as one of the major controlling factors for bacterial community structure and diversity (Chong et al. 2009, 2010, 2012). In contrast, another study found no relationship between moisture, soil particle size, salinity, pH, and bacteria abundance (Line 1988). Bird's presence and identity have also recently been reported as significantly influencing microbial communities (Teixeira et al. 2013).

Plants are known to produce soil microhabitats (Kowalchuk et al. 2002), and some reports have demonstrated that unvegetated polar soils generally support fewer microbes than soils associated with mosses (Kaštovská et al. 2005; Yergeau et al. 2007a). It was suggested that for Antarctic fell-field soils, this may be caused by the combined effects of greater nutrient availability and more favorable physical conditions (Harris and Tibbles 1997). However, these studies were confounded by the fact that dense vegetation occurred at sheltered sites that already experienced relatively stable water and temperature conditions. Dense vegetation was able to counter the effects of extreme environmental conditions to some extent, which resulted in disparate effects of increasing latitude on bacterial abundance in densely and sparsely vegetated fell-field soils (Yergeau et al. 2007a). There is also some evidence suggesting a rhizospheric influence on microbial communities with more *Actinobacteria* and *Firmicutes* relative to *Acidobacteria* associated with the rhizosphere of *Colobanthus quitensis* and *Deschampsia antarctica* (Teixeira et al. 2013). In contrast, another study, using a different methodology, did not find any evidence of a rhizosphere effect for *D. antarctica* (Teixeira et al. 2010).

It is generally accepted that the harshness of Antarctic environments may not be caused by extreme climatic conditions *per se,* but more to the extreme range of conditions that are encountered. Antarctic terrestrial bacteria are believed to be cold-tolerant as opposed to cold-adapted (Line 1988; Wery et al. 2003; Aislabie et al. 2006). This may not be surprising since cold-tolerant organisms are better adapted than true cold-adapted microorganisms to survive the large and frequent temperature variations that occur in Antarctica (Cowan and Ah Tow 2004). This also implies that the selection pressure for low optimal growth temperature is relatively low compared with that of other environmental constraints (Vincent 2000). Interestingly, bacterial abundance was reported to not simply decrease with the coldness of the environment, but was also influenced by freeze–thaw cycle frequency (Yergeau et al. 2007a). Freeze–thaw cycles may actually impose a greater degree of stress than conditions with colder average temperatures (Yanai et al. 2004; Yergeau and Kowalchuk 2008).

7.2.2 Community Composition

Recent data from three Antarctic cold desert mineral soils revealed low-diversity communities containing a high proportion of novel, potentially psychrotrophic taxa (Smith et al. 2006). In contrast, bacterial community diversity and composition in vegetated soils was rather similar to that of soils from temperate environments, and this was thought to be related to the fact that Antarctic soils associated with plant growth offer relatively stable and nutrient-rich environments (Harris and Tibbles 1997). Bacterial community composition also differs markedly between mineral and densely vegetated fell-field soils. Indeed, in a bacterial 16S rRNA gene clone library study along a latitudinal transect, the mineral fell-field sites located at the southern limit of the Antarctic Peninsula were remarkably different from those observed from sites in the northern part of the Peninsula, which were mainly composed of pink-pigmented methylotrophic bacteria (*Methylobacterium*) or *Sphingobacteriales* (Yergeau et al. 2007c). These sites are characterized by extremely low inputs of nutrients, exposure to high levels of UV radiation in summer, and low and transient water availability, which impose strong selective pressures on these communities. Previous studies have reported the presence of these bacterial groups in Antarctic soils (Moosvi et al. 2005; Romanovskaya et al. 2005; Aislabie et al. 2006) and other cold environments (Christner et al. 2001; Trusova and Gladyshev 2002; Segawa et al. 2005). *Methylobacterium* sp. has been reported to have a high resistance to desiccation and UV radiation (Romanovskaya et al. 1998, 1999, 2002). Similarly, other mineral fell-field soils were reported to be dominated by a relatively narrow range of bacteria, and these groups varied depending on sampling location. The dominant phylum was either *Actinobacteria* (Dry Valleys) or *Bacteroidetes* (Victoria Land); (Aislabie et al. 2006; Smith et al. 2006). The presence of the above-mentioned groups in mineral soils may be a function of their specific metabolic capacities, which coupled with cold and drought hardiness, may give these bacteria an advantage over other groups when nutrients are limiting.

Autotrophic bacteria would be expected to dominate sparsely vegetated fell-field soils due to the low input of nutrients in this system. Cyanobacterial community structure might be dictated to some degree by the presence of mosses, with one study demonstrating an association of specific cyanobacterial assemblages with mosses (Solheim et al. 2004). Cyanobacteria were also reported to be highly diverse and abundant in several Antarctic mineral soils (Christie 1987; Bölter et al. 1997; Smith et al. 2006; Brinkmann et al. 2007). However, recent molecular work across a range of Antarctic Peninsula fell-field soils suggests that Cyanobacteria only make up a small minority of these bacterial communities (Yergeau et al. 2007c, 2009, 2012) and were even reported to be below PCR detection limits (Yergeau et al. 2007a). Relatively low proportions of autotrophic bacteria were also reported in the Antarctic Dry Valleys (Moodley 2004). Interestingly, a study that specifically targeted cyanobacteria showed a relatively high diversity in Coal Nunatak polygons (Brinkmann et al. 2007), although density and total activity were probably very low. Given these mixed results, it is still unclear which environmental factors promote cyanobacterial presence and activity across Antarctic habitats.

The rhizosphere of *D. antarctica* and *C. quitensis* has been reported to be dominated by *Firmicutes* (Teixeira et al. 2010) or *Actinobacteria* (Teixeira et al. 2013), while densely vegetated fell-field soils along the Antarctic Peninsula were dominated by either *Actinobacteria*, *Acidobacteria* or *Alphaproteobacteria* (Yergeau et al. 2007c, 2012). In contrast, fell-field soils from Signy Island were dominated by the *Bacteroidetes* (Chong et al. 2009, 2010).

7.2.3 Diversity

It has been hypothesized that the large population sizes and high distribution potential of microorganisms might lead to many cosmopolitan species and generally high levels of microbial diversity (Vincent 2000; Finlay 2002; Tindall 2004). Despite the extreme isolation of Antarctic and sub-Antarctic habitats, such a scenario is supported by the demonstration that biological material can be transported aerially to the Antarctic Peninsula from South America or other Antarctic locations (Marshall 1996; Hughes et al. 2004). In line with this general idea, a study of the micro-eukaryote diversity across a range of Antarctic terrestrial sites revealed no clear pattern of decreasing diversity with latitude (Lawley et al. 2004), and similar findings have been reported for tardigrades and rotifers (Sohlenius and Boström 2005). Alternatively, increasingly stressful environmental conditions have been hypothesized to act as strong selection factors, thus limiting the biodiversity of soil organisms, and trends toward lower diversity at higher Antarctic latitudes have been observed for protozoa (Smith 1992; Wynn-Williams 1996), nematodes (Sohlenius and Boström 2005), and algae (Wynn-Williams 1996). It could be argued that the severity of an environment is not as important to the development and maintenance of biodiversity as environmental stability (Peck et al. 2006). Stable environments are thought to help support a higher degree of organization, more complex food webs, more niches, and ultimately more species.

Although several culture-independent molecular studies have examined Antarctic bacterial diversity in lakes (Pearce et al. 2003, 2005), pack ice (Brinkmeyer et al. 2003), sediments (Sjoling and Cowan 2003), and soils (Aislabie et al. 2006; Smith et al. 2006), very few have looked specifically at bacterial diversity patterns in Antarctic fell-field ecosystems. In one of the few molecular surveys of bacterial diversity in Antarctic terrestrial environments, it was reported that the extremely harsh environments of three different Antarctic cold desert mineral soils contained bacterial communities of relatively low diversity (Smith et al. 2006). Similarly, using a 16S rRNA taxonomical microarray, Yergeau et al. (2009) showed that the number of bacterial and archaeal taxa detected in Antarctic fell-field soils was lower than previously reported for similar analyses of temperate soil environments (Brodie et al. 2006; DeSantis et al. 2007). The diversity of bacteria in unvegetated fell-field soils was reported to decrease with increasing latitude (Yergeau et al.

2007c, 2009). These results are in line with the majority of surveys of Antarctic flora and fauna conducted over the past number of decades, which reported decreased diversity with increasing latitude (Greene et al. 1967; Rudolph 1971; Block 1984; Smith 1984, 1992; Wynn-Williams 1996; Convey 2001; Clarke 2003; Sohlenius and Boström 2005; Peat et al. 2006).

In contrast, no negative diversity/latitude relationship was observed for samples collected under dense vegetative cover (Yergeau et al. 2007c) and barren fell-field soils that were reported to harbor lower diversity than vegetated soils (Chong et al. 2009). Vascular plants, and to a lesser extent bryophytes, are known to select for specific soil-borne microbial communities, which would serve to reduce bacterial diversity and evenness in the rhizosphere (Smalla et al. 2001; Kowalchuk et al. 2002; Opelt and Berg 2004). The strength of this selection decreases as the interactions between vegetation and soil become more rudimentary while the physical protective effects of vegetation (Harris and Tibbles 1997; Yergeau et al. 2007a) might be expected to become more important in reducing climate-induced selection as the climate becomes more severe.

7.3 Fungi

7.3.1 Influencing Factors

Similar to bacteria, numerous studies have reported a prevalence of cold-tolerant rather than cold-adapted fungi in Antarctic soils (Kerry 1990; Melick et al. 1994; Zucconi et al. 1996; Robinson 2001). Fungi isolated from Antarctic regions were reported to have optimum growth temperatures of 12–20 °C (Del Frate and Caretta 1990; Azmi and Seppelt 1998; Tosi et al. 2002). It is not surprising to find fungi with relatively high optimal growth temperatures, since fungi have numerous ways to resist to cold temperatures. For instance, fungi can avoid harsh temperatures through annual germination of spores and by long and short distance dispersal from other environments (Robinson 2001). Interestingly, along a latitudinal gradient, the fungi-to-bacteria ratio was reported to be the highest at sites with the harshest temperatures (Yergeau et al. 2007a). This could imply that fungi are less influenced by weather conditions than that of bacteria and can more easily dominate in harsh ecosystems, probably due to superior adaptation to lower temperatures.

Since Antarctic fungi are optimally adapted to conditions that are warmer than those currently encountered in Antarctic habitats, temperature and soil moisture are the major controlling factors of fungal diversity, community structure, and biomass. Fungal diversity was found to be higher in sub-Antarctic islands where the climate is more humid and more temperate (Smith 1994a; Azmi and Seppelt 1998), and a study using modern molecular tools reported a strong differentiation in diversity between continental and maritime sites (Lawley et al. 2004). Seasonal variability in fungal and yeast biomass has also been coupled to patterns of humidity and temperature (Wynn-Williams 1982). Cultivable fungal abundance at different Antarctic fell-field sites was also strongly influenced by organic matter and soil water content (Bailey and Wynn-Williams 1982), while community structure was related to the species composition of the overlying vegetation (Smith and Walton 1985). One study reported that fungal community structure and abundance was not influenced by plant cover *per se,* but by the interaction between location and vegetative cover, suggesting that the type of vegetation influenced the effect of latitude on fungal communities (Yergeau et al. 2007a). In line with this observation, fungal communities were found to respond very differently to changes in organic input levels and quality depending on environmental conditions (Tosi et al. 2005). These studies lend some support to the notion that fungal communities can also be shaped by substrate quality and quantity, as well as other site-specific characteristics, as opposed to pure weather-related parameters.

7.3.2 Community Composition

Antarctic fungal diversity has been surveyed for many decades (Pegler et al. 1980; Pugh and Allsopp 1982; Gray and Smith 1984; Line 1988; Del Frate and Caretta 1990; Smith 1994a; Azmi and Seppelt 1998; Tosi et al. 2002; Jumpponen et al. 2003; Lawley et al. 2004; Tosi et al. 2005). However, most of these studies have been restricted to a single site and were aimed at the discovery of new species. Some highly valuable information can still be extracted from these studies on the whole. For instance, sites near scientific stations were reported to have fungal genera that were not found in other undisturbed sites (Azmi and Seppelt 1998), and similarly, sites affected by birds provided conditions that were more favorable to the development of soil fungi (Tosi et al. 2005). Higher fungi from a range of Antarctic habitats were remarkably similar to temperate and Arctic fungi, suggesting a cosmopolitan distribution or possible introduction by anthropogenic factors (Pegler et al. 1980). However, the high stress and disturbance conditions of Antarctica may select for species that produce a large number of small spores as a survival strategy (Tosi et al. 2005). Arbuscular mycorrhizal fungi have not been detected in Antarctic ecosystems (Christie and Nicolson 1983; DeMars and Boerner 1995; Malosso et al. 2004) but were present on sub-Antarctic islands (Christie and Nicolson 1983; Smith 1994a). Lower plants, which dominate Antarctic flora, also have the capacity to form symbiotic fungal associations (Read et al. 2000), and in fact, colonization by *Ascomycetes* and ericoid mycorrhizal fungi has been observed in liverworts and hepatic specimens of Antarctica (Williams et al. 1994; Upson et al. 2007).

7.4 Biogeochemical Cycles

Bacteria and fungi are key players in most nutrient cycles (Prosser 2007), and it is thought that their importance in nutrient cycling is more substantial in Antarctic fell-field environments than temperate environments. Indeed, due to a principle lack of insect and mammalian herbivores and detritivores at most locations (Smith and Steenkamp 1992), food webs are primarily driven by bacterial and fungal detritus-based pathways (Smith 1994a). Even with these relatively large nutrient inputs, N was still reported as limiting in Antarctic ecosystems (Mataloni et al. 2000). However, this might not be the case in densely vegetated maritime Antarctic fell-field soils where high N contents have been observed (Bokhorst et al. 2007a), which is in some cases caused by bird's input (Bokhorst et al. 2007b).

7.4.1 Nitrogen Cycle

It has been reported that the main sources of nitrogen in Antarctic soils are bird's droppings (Christie 1987; Bokhorst et al. 2007b) and N_2-fixation (Ino and Nakatsubo 1986). N_2-fixation in Antarctica has been suggested to occur through the action of free-living N_2-fixing bacteria and the cyanobionts of lichens (Line 1992; Adams et al. 2006; Yergeau et al. 2007b). Heterotrophic N_2-fixation has not been detected as a significant source of reduced nitrogen (Pandey et al. 1992), probably due to energy limitations (Christie 1987). Thus, Cyanobacteria are believed to be the major N_2-fixing organisms in Antarctic environments (Ino and Nakatsubo 1986; Line 1992; Vishniac 1993), with their contribution to N_2-fixation reported to be four times greater in wet habitats than dry ones (Christie 1987). However, this group was only found at low levels in 16S rRNA gene libraries from a variety of fell-field soil samples (Yergeau et al. 2007c) and among a range of different Antarctic soils. The highest rates of N_2-fixation have been reported for relatively dry nunatak soils (Pandey et al. 1992). Similarly, using a functional gene microarray and real-time PCR, N_2-fixing genes were detected in fell-field soils, with higher abundances in soils with lower vegetative cover (Yergeau et al. 2007b).

In the few studies that have investigated the other N_2-cycle steps in Antarctic habitats, Signy Island habitats have been reported to be devoid of ammonia-oxidizing bacteria (Vishniac 1993). This contrasts with a recent report that detected ammonia monooxygenase genes in a range of fell-field soils, including Signy Island, using functional gene microarrays (Yergeau et al. 2007b). For all fell-field soil samples examined, the genetic potential for complete denitrification (from NO_3^- to N_2) has been detected (Yergeau et al. 2007b), but nitrifying bacteria were reported to outnumber denitrifying bacteria, suggesting N conservation in some Antarctic soils (Christie 1987). A recent study suggested that one of the two native Antarctic vascular plants, *D. antarctica,* has the ability to successfully compete with both soil microbes and moss for proteinaceous N at an early stage of decomposition (Hill et al. 2011), which could further increase N limitation for microorganisms.

7.4.2 Carbon Cycling

One of the distinctive features of Antarctic terrestrial ecosystems with respect to the C-cycle is the absence of mammalian and insect herbivores and detritivores (Smith and Steenkamp 1992). The consumption of algae by primary consumers is the only significant herbivory, with less than 0.1 % of the net primary production by bryophytes and lichens being consumed due to their poor nutritional quality (Davis 1981). Decomposition in Antarctic soils is carried out mainly by bacteria, microfungi, yeast, and probably to some extent by *Basidiomycetes* when present (Smith 1994a). It is believed that fungi are the dominant decomposers in Antarctica, in contrast to the Arctic where bacteria are presumed to dominate this process (Walton 1985). In nutrient-poor Antarctic ecosystems, microbial C-fixation could be an important input of C to the soil (Vincent 1988; Hopkins et al. 2006).

Several factors have been reported to influence the C-cycle in Antarctic environments. These can be classified into two main categories: vegetation-related (quality and quantity of organic matter, soil moisture content) and latitude-related (temperature, freeze–thaw cycles); (Davis 1981; Walton 1985). Vegetation type is thought to play an important role in driving microbial decomposers. In South Georgia (maritime Antarctic), marked differences in cellulose degradation were observed under different vegetation (Walton 1985). The distribution of C-cycle genes that were detected on a functional gene microarray was also reported to be significantly affected by vegetation cover (Yergeau et al. 2007b). The effect of vegetation cover was probably due to differential input of carbohydrates to soil via exudation, “root” turnover and litter. Importantly, the major soluble carbohydrates in vascular plants, bryophytes, and lichens are different (Melick and Seppelt 1992; Roser et al. 1992; Melick et al. 1994). Microbial decomposition is very sensitive to soil water content and to variations in oxygen conditions, with the slowest rates of decomposition occurring in water-logged and anaerobic conditions (Davis 1986; Smith and Steenkamp 1990; Kennedy 1995).

The quantity and quality of C inputs into soil can also be affected by environmental conditions. For instance, the photosynthetic activity of mosses was shown to recover more slowly from cold periods when compared with lichens (Schlensog et al. 2004). Temperature has previously been identified as a key determinant of cellulase activity and decomposition rates (Pugh and Allsopp 1982; Kerry 1990), and the total relative abundance of cellulase genes decreased with increasing latitude (Yergeau et al. 2007b). Similarly, seasonal changes in carbon-cycle processes have been reported, whereby dissolved organic compounds were used mainly in spring and autumn while more complex organic compounds were used in summer (Wynn-Williams 1980). Freeze–thaw cycles are also believed to play an important role in C-cycling in the Antarctic, not only due to the stress imposed on microbial communities, but also because they induce changes in the exudation patterns of cryptogams (Tearle 1987; Melick and Seppelt 1992, 1994). It has estimated that each year freeze–thaw cycles induced the release of >15 % of the total organic matter of Antarctic cryptogams to the soil *microbiota* (Tearle 1987), while only 1.5 % of plant material becomes available each year through the breakdown of dead subsurface material (Davis 1986). Accordingly, the frequency of freeze–thaw cycles was identified as a potential driving factor for the structure of the microbes involved in the C-cycle (Yergeau et al. 2007b).

7.5 Conclusion

Antarctic fell-field soils are spectacular in terms of the diversity of conditions that they offer for microbial life. This is reflected in the variety of microbial taxa and functions that can be found in these environments. Several factors were identified as having strong influences on the microbial communities inhabiting Antarctic fell-field soils, including water, temperature, plants, birds, and pH. Most of these factors are expected to change with ongoing climatic changes, and as such, the face of fell-field microbial communities might drastically change over the following decades. This is further examined in Chap. 13.

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Chapter 8
Biological Soil Crusts

Burkhard Büdel and Claudia Colesie

Abstract Biological soil crusts (BSC) live in the upper millimeters of the soil and are composed of bacteria, algae, fungi, lichens, and bryophytes in different proportions. They occur in arid environments of the Earths or wherever an arid microclimate is realized. BSCs increase soil stability, resistance to erosion, and soil fertility. While for single groups of soil inhabiting cryptogams (including bacteria) a number of studies exist, the concept of biological soil crusts is not well established for Antarctica yet. Here we summarize knowledge about Antarctic BSCs from our own work and from literature, the latter being especially searched for descriptions of photoautotrophic communities that can be interpreted as BSCs.

8.1 Introduction

Biological soil crusts (BSC) are unique communities of cryptogams like cyanobacteria, algae, fungi, lichens, and bryophytes living in the upper few millimeters of the soil, which associate in different proportions and compositions. They occur in arid regions or wherever an arid microclimate is realized (Pointing and Belnap 2012). In such regions, BSC can improve the stability of soils and the resistance to soil erosion by wind increases with BSC development, independent of the substrate. BSC also increase soil fertility and influence hydrological cycles (Belnap and Lange 2003). The effects of various types of BSC have been well studied, and it is in nutrient- or water-poor environments that they make their greatest impact. The photoautotrophic components of the BSC can underpin the trophic hierarchy by leaching carbon into the soils

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(Dudley and Lechowicz 1987) and serving as a food resource. Cyanobacteria as BSC components can also fix atmospheric nitrogen and supply this to the communities. These ecosystem services are of special importance in areas where the influences of higher primary producers are low. Although a number of reviews dealt with terrestrial cryptogamic organisms from Antarctica (e.g., Adams et al. 2006; Broady 1996, 2012; Namsaraev et al. 2010; Seppelt 2002; Green et al. 2007), to our knowledge, only one was devoted to Antarctic BSC (Green and Broady 2001).

Biogeographical descriptions of vegetation are ideal for studying abiotic mechanisms that control ecosystem structure and function. Ecosystems in Antarctica are of a special character as they are considered being the harshest environments on earth with low summer temperatures and a very short growing season, a strongly seasonal climate in addition with very low precipitation falling as snow, and high sublimation rates that further limit the availability of water and provide yet more problems for life. Under these conditions, the study of biogeographic vegetation patterns is of special interest as the vegetation is at its physiological limit of survival, when slight changes can have large impacts on sensitive terrestrial communities like BSC.

8.2 Biogeography

Biogeographical patterns of cryptogamic communities have been studied since Stephenson described the first Antarctic oasis in 1938. The oasis concept was later well established (Pickard 1986) but is nowadays antiquated. The concept of dividing Antarctica into three different phytogeographic zones (continental, maritime, and periantarctic) is now widely used and well reviewed in Robinson et al. (2003). This classification is based on the very distinct climatic conditions, resulting in different types of water availability for the vegetation. Water is the crucial factor influencing vegetation distribution throughout the continent (Kennedy 1993) and influences the growth of organisms (Pannewitz et al. 2003). Plant diversity and biogeography in the humid maritime Antarctic is reviewed in Peat et al. (2007), leading to the idea that distribution patterns follow a latitudinal gradient. For BSCs in continental Antarctica, there is no discrete review compendium of distribution patterns available, despite the review by Green and Broady (2001). Here, we focus on the description of distribution patterns, based on this review, and enumerate BSC formations in three different geographic zones of the Antarctic continent per se.

8.2.1 Dronning Maud Land

Dronning Maud land ranges between the Stancomb-Wills Glacier at 20°00′W to the Shinnan Glacier at 44°38′E, which includes the Schirmacheroasis, the Gjelsvikfjella, and the Mühlig-Hofmannfjella mountain ridges. Moss formations are the most eye-catching cryptogam communities in this region, and their distribution patterns are reviewed in Kanda et al. (2002). For Yukidori Valley, which is considered to have one of the most prominent vegetation cover in Dronning Maud Land (Ohtani and Kanda 2002), three types of moss formations are distinguished. Firstly, the *Ceratodon purpureus* (Hedw.) Brid. subassociation, which spreads widely over the valley and is most abundant in the drier parts of the valley center (Okitsu et al. 2003). Secondly, the *Bryum pseudotriquetrum* (Hedw.) G. Gaertn. subassociation, which is the dominating moss formation in the valley. Lastly, the *C. purpureus*–*B. pseudotriquetrum* subassociation is mainly found along streams and lakes (Okitsu et al. 2003). The colony structure of these mosses is described in Kanda et al. (2004) who also highlights interactions between mosses and other cryptogams living epiphytically on the mosses. From 50 moss samples, only 20 were found to grow without accompanying organisms. All other moss samples grew together with either cyanobacteria or lichens. Within the Swoya region, 25 lichen species were known in 1991 (Inoue 1991), but only the soil-inhabiting organisms can be considered being part of BSC. Lichen distribution is controlled by water availability; however, in this special case also wind-blown sea spray and the influence of bird nests have to be considered (Inoue 1989). From 32 described lichen species in 1995, only 27 are described to grow on gravel (Inoue 1995) and can possibly contribute to biological soil crust formation.

In other habitats of Dronning Maud land like the Mountains of Grjelsfjella and Mühlig-Hofmannfjella, fruticose lichens are mainly epilithic (Engelskjøn 1986) and are classified according to thallus morphology. Open soil, like charnockite, and gneiss gravel can be the substratum for moss associations like the *Grimmia lawiana* J. H. Willis or the *Sarconeurum glaciale* (C. Muell.) Card. et Bryhn associations. The first of these associations is often accompanied by the lichen *Lepraria angardiana* Øvstedal and cyanobacteria like *Stigonema*, *Chroococcus*, *Scytonema*, and *Synechococcus* species (Engelskjøn 1986).

Cyanobacteria and green algae also associate to form BSC. Altogether, 42 genera of soil algae and cyanobacteria were described in different studies in the vicinity of Swoya station, including Ongul Island and Langhovde (Kanda et al. 2002). Cyanobacteria like *Nostoc* or the green alga *Stichococcus* were found at all investigation sites. The green alga *Prasiola crispa* (Lightfoot) Kützing was reported to form large soil covers at eutrophic sites near penguin rookeries (Kanda et al. 2002). Despite this, there are also recordings of *Prasiococcus calcarius* (J. B. Petersen) Vischer for Mc. Robertson Land for several diverse habitats (including soil adjacent to bird nesting areas and raw mineral soil) (Broady 1983). Macroscopic colonies of cyanobacteria extend across the wet soil surfaces along meltwater streams for example *Nostoc commune* Vaucher ex Bornet and Flahault in the Yukidori Valley (Kanda et al. 2002) or *Calothrix braunii* Bornet and Flahault and *Cyanothece aeruginosa* (Nägeli) Komárek in the Schirmacheroasis (Pankow et al. 1991).

The ecology and distribution patterns of terrestrial photoautotrophic communities of the Schirmacheroasis are reviewed in the monograph from Pankow et al. (1991). The author describes cyanobacteria-dominated soil crusts as a typical component of perpetually wet soils along meltwater streams or lakes. The nitrogen input from these communities as well as the potential nutrient supply for co-occurring lichens like *Xanthoria elegans* (Link) Th. Fr or *Physcia caesia* (Hoffm.) Fürnr. is discussed. It is hypothesized that the growth of co-occurring cyanobacteria has a stronger impact on mosses than on lichens in the Schirmacheroasis. Cyanobacteria are thought to cover mosses beyond recognition after which these mosses and cyanobacteria are then covered with epiphytic lichens. Pankow et al. (1991) also describes mosses, algae, cyanobacteria, and even lichens growing within the uppermost millimeters of the fine gravel on open soils. This very inconspicuous niche is thought to offer both radiation protection and a reliable water supply due to the special hydrochemistry of loose gravel suitable for the soil dwelling organisms.

8.2.2 Wilkes Land (Windmill Islands)

Wilkes Land reaches from Queen Mary coast to Adelieland and is predominantly snow covered year round. Major studies on vegetation were conducted at the Windmill Islands, divided into two parts, the southern windmill islands comprised of the Browning Peninsula, Holl Island, and Herring Island and the northern part the Robinson Ridge, Mitchell, Bailey, and Clark Peninsula. Wilkes Land supports the most extensive vegetation cover of any continental Antarctic locality (Seppelt 2002). Vegetation distribution on ice-free areas shows great variation, with the northern peninsulas being colonized by bryophyte and lichen communities and the southern island with poorly developed vegetation (Melick et al. 1994), having fewer species and less coverage. Up to only 10 lichen and 2 moss species occur in the southern region where their occurrence is generally rare and only on barren rock (Melick et al. 1994). In contrast, the presence of well-developed vegetation communities in the northern part of the Windmill Island has led to the designation of the Sites of Special Scientific Interest (SSSI). Numerical analyses of the vegetation revealed four major vegetation groups (Melick and Seppelt 1997: (1) the pure bryophyte community, which can be considered a biological soil crust composed of *Grimmia antarctici* Cardot, *C. purpureus,* or *B. pseudotriquetrum*; (2) the transitional bryophyte communities, which are combined by the fact that there is bryophyte development but can be dominated by either crustose lichens (*Rinodina olivaceobrunnea* C. W. Dodge and Baker*, Buellia grimmiae* Filson, or *Candelariella flava* (Dodge et Baker) (Castello et Nimis)) or by foliose lichens (*Usnea/Candelariella flava/Pseudephebe minuscula* (Nyl. ex Arnold) Brodo and D.Hawksw, *Usnea sphacelata* R.Br, or *Usnea antarctica* Du Rietz); (3) the nutrient-enriched lichen communities with *X. elegans*, *X. mawsonii* C. W. Dodge, *Caloplaca citrina* (Hoffm.) H. Olivier, *Candelariella flava,* and *Buellia frigida* Darb at eutrophic saline areas; (4) the established macrolichen communities with extensive mats of *U. sphacelata*. These four cryptogam communities have been described as shifting between each other with changes in exposure and wet–dry cycling, from crustose lichens colonizing the moribund bryophytes under moist and less exposed conditions to the dominant macrolichen communities under the harshest conditions (Melick and Seppelt 1997). The broad-scale distribution pattern at Windmill Island suggests an ongoing expansion of the lichen-dominated soil crusts with a contraction of the bryophyte communities (Seppelt 2002). This pattern correlates with the climate in this region, which has become drier in recent decades, caused by an isostatic uplift of the region since the last deglaciation (Seppelt 2002). Other studies show that the abundance of terrestrial vegetation in the region is directly correlated neither to the thermal regime, nor to soil properties. The author suggests ecological parameters such as moisture availability to determine the distribution patterns (Beyer et al. 2000).

Besides the macroscopic BSC, there are only a few comments about algal-dominated crusts. In 1983, Broady described *P. calcarius* on raw mineral soil but also on soil adjacent to bird colonies in the Vestfold Hills. At other eutrophic sites, where the macroscopic crusts are absent, soil crusts are dominated by green algae like *P. crispa*, *P. calcarius,* and *Desmococcus olivaceus* (Persoon ex Acharius) (Seppelt 2002). Cyanobacteria were also found to grow in the vicinity of penguin colonies, like *Oscillatoria* sp., which forms a dark brown felt (Ling and Seppelt 1998). On damp mineral soil, fine sand, and frost boils, other cyanobacteria (*Synechococcus, Stigonema, Gleocapsa, Katagnymene,* and occasionally *Chroococcus)* form reddish brown and black crusts (Ling and Seppelt 1998).

8.2.3 Victoria Land

Victoria Land includes the region bound to the east by the Ross Ice Shelf and the Ross Sea, and by Oakes and Wilkes Land in the west. From north to south, Victoria Land includes several perpetually ice-free areas like Cape Adare, Cape Hallett, the Admiralty Range, Granite Harbour, the McMurdo Dry Valleys, the La Gorce Mountains, Shackleton Range, and the Queen Maud Mountains. Within the broad range of Victoria Land, Adams et al. (2006) reviewed the studies of taxonomy and distribution and deduced that the remaining gaps in contemporary knowledge prevent confident biogeographical analyses and patterns. Therefore, we describe the nominations of BSC or potential BSC-forming organisms, by regarding single habitats from north to south with only few previous general comments. Algae and cyanobacteria are present in almost all ice-free areas of Victoria Land; they occur in soils, as epiphytes on mosses, as cyanobacterial mats, and planktonic in lakes and ponds (Adams et al. 2006). The bryophyte and lichen flora is not rich, and the degree of endemism is lower than formerly supposed (Adams et al. 2006). Factors like soil microclimate, organic matter, moisture, and salinity are besides broad-scale gradients, like distance to the coast, latitude, and soil chronosequences described being the primary controls over structure of soil communities and their functioning (Barrett et al. 2006).

The vegetation at Cape Hallett (72°18′S) was classified into three components by Rudolph (1963). The author described an algal-dominated "soil component" covering 12.8 % of the area (mainly in moist habitats) which was composed of *P. crispa*, associated with other green algae and cyanobacteria that were not described in detail. The second consisted of *Bryum argenteum* Hedw., covering 2.4 %, which is dominant where the water level is at the surface or slightly below the gravel substrate. The third consisted of lichens such as *Xanthoria mawsoni, Parmelia coreyi* Dodge and Baker, *C. citrina,* and *B. frigida*. As this type has been described as typical for drier sites, it also had the lowest coverage with only 0.2 %. In other sites of northern Victoria Land, for example, the Luther Vale (72°22.268 S) at the eastern end of Admiralty Range, cyanobacteria were recently found as a part of an unexpected soil biodiversity (Niederberger et al. 2008). In association with other photoautotrophic organisms, cyanobacteria and green algae are found to grow epiphytically on mosses with a comparatively high diversity (24 cyanobacteria, 6 green algae; Alfinito et al. 1998). Further south at the Kar Plateau (76°53′S), species numbers were also much higher than previously expected (Seppelt et al. 1995). Twenty-two lichen and five moss species were found, although the majority grow on rock surfaces and cannot be considered as BSC components. Accordingly, debris islands in this chaos of rocks (felsenmeer) are reported to have very low vegetation coverage with only a single moss species (*B. argenteum*) covering about 1 % of the area. The lack of an extensive moss cover results in epiphytic lichens such as *C. citrina* and *Lecanora expectans* being apparently rare on the Kar Plateau (Seppelt et al. 1995). In contrast, a few kilometers further south at Botany Bay, Granite Harbor vegetation is described as one of the richest sites for lichens and bryophytes (Seppelt et al. 2010). One liverwort, nine mosses and at least 30 lichen species are documented by an intensive survey along different gradients (Seppelt et al. 2010). The vegetation was classified at the subassociation level, with five growing on soil that can be considered being BSC here. Two of them are named after the most frequent lichens, which are the *Xanthomendoza borealis* (R. Sant and Poelt) Søchting, Kärnefelt, and S. Kondr and the *C. citrina* subassociations, the first occurring on sandy gravel and coarse sandy soils with considerable ornithogenic nutrient input and the second on moss cushions and turfs, but with the nitrophilous lichens being dominant. Additionally, there were two moss subassociations. The third, *B. argenteum–B. pseudotriquetrum* subassociation which is strongly associated with meltwater streams and pools, and the fourth, the *C. purpureus* subassociation occurred on sandy or silty soils among moraine debris. *C. purpureus* itself showed a very high genetic variability within and among colonies (Skotnicki et al. 2004). Algal-dominated crusts seem to be rare in this area, with *P. crispa* covering only 1.8 % (Seppelt et al. 2010).

In the McMurdo Dry Valleys, epilithic lichen species, including *Acarospora gwynii* C. W. Dodge and Rudolph, *B. frigida*, and *Carbonea capsulata* (C. W. Dodge and G. E. Baker) Hale are found primarily in protected niches beneath the rock surface (endolithic; Adams et al. 2006), which reflects the extreme desert conditions in this area. Although the identification of lichens is difficult because of the presence of numerous sterile and extremely modified thalli from maritime climate-influenced Valleys, like the Garwood or Miers Valley (Fig. 8.1), up to 15 lichen species could be identified (Pérez-Ortega et al. 2012). However, their

Fig. 8.1 Garwood Valley, view toward Garwood Lake, Joyce Glacier (*background*), and Péwé Peak (*centre left*)

contribution/relation to BSC remained unclear. Colesie et al. (2013) described BSC in Garwood Valley being composed by both lichens (*X. elegans*, *L. expectans*) and mosses (*Hennediella heimii*; Figs. 8.2 and 8.3). Mosses like *H. heimii* (Hedw.) Zand. or *B. argenteum* are reported to occur in Garwood Valley, but with an extensive genetic variation, with no two samples being identical in either species (Selkirk et al. 1998). In Victoria Valley, soil-inhabiting lichens and bryophytes are entirely absent (Green and Broady 2001). In Taylor Valley, *B. argenteum* occurs along meltwater streams and seepage sites (Figs. 8.4, 8.5, 8.6, 8.7), or on drier sites where it is often replaced by *Henediella heimii* (Schwarz et al. 1992). Both mosses occur together with cyanobacteria, apparently the most abundant phylum in the Dry Valleys. In Victoria Valley, they form dark brown to black granular crusts encountered over surfaces of mineral soils (Broady 2005), while in Taylor Valley, they form mats around lakes (e.g., Lake Fryxell; Michaud et al. 2012), or occur on barren soil (Michaud et al. 2012). Culture-independent studies revealed cyanobacteria as the only photoautotrophic component in open soils at Marble Point and Wright Valley (Aislabie et al. 2006). Diverse cyanobacterial communities exist within the mineral soils of Miers Valley (Wood et al. 2008). However, even by using state-of-the-art techniques, some soils lack significant photoautotrophic components, for example, the McKelvey Valley (Pointing et al. 2009) or Beacon Valley (Wood et al. 2008). High light intensity, high incident UV, rapid high amplitudes of humidity and thermal fluctuations, low water availability, low atmospheric CO_2 concentrations, and physical instability force organisms to protect themselves; most of them retreat to the cryptoendolithic ecological niche (Büdel et al. 2009; Cary et al. 2012; Cowan et al. 2010).

At latitudes higher than about 72°S, biodiversity becomes confined to microhabitats and no longer follows broad-scale gradients (Green et al. 2011a, b). Further south to the Dry Valleys, this "*microenvironment*" zone uncouples biodiversity richness from the macroenvironment and determines occurrence of life to occasional coincidences (Green et al. 2011a). At the Darwin Mountains (80°S), Magalhães et al. (2012) described cyanobacteria occuring in 17 out of 30 soil

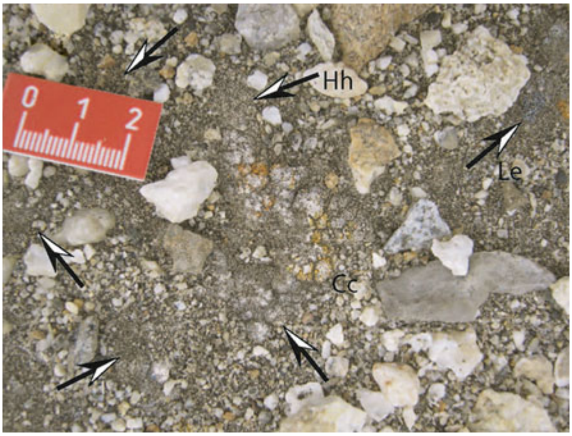


Fig. 8.2 Bryophyte—lichen crust with *Henediella heimii* (Hh), *Caloplaca citrina* (Cc), and *Lecanora expectans* (Le); *arrows* indicate crusts

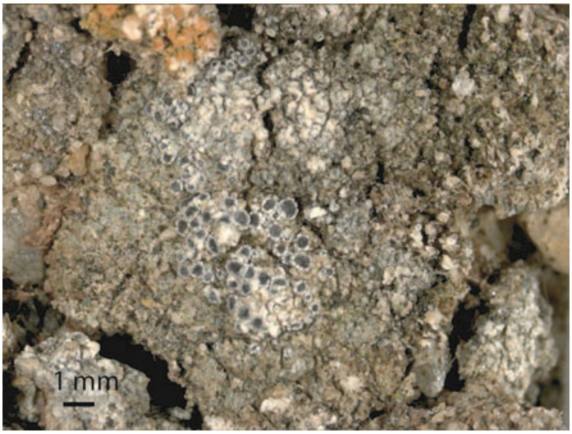


Fig. 8.3 *Lecanora expectans* on top of mosses, habitus with black apothecia

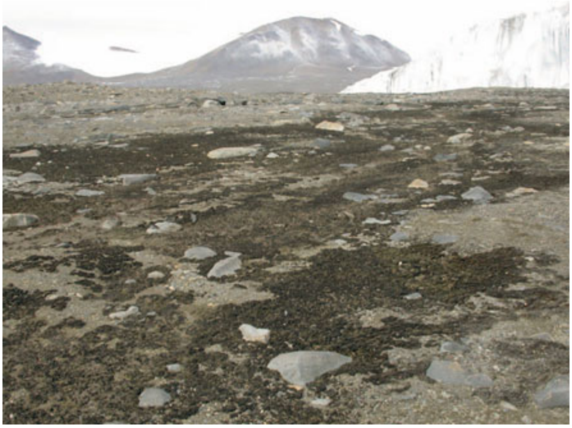


Fig. 8.4 Bryophyte flush next to the Canada Glacier (*right*), Taylor Valley

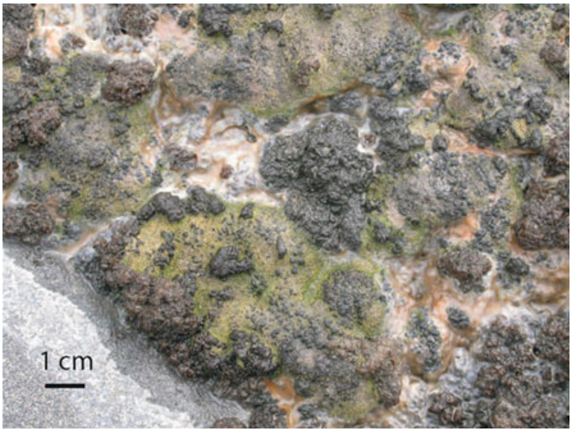


Fig. 8.5 *Bryum argenteum* (*green*)—*Nostoc commune* (*brownish black cushions*) crust aside meltwater stream of the Canada Glacier

Fig. 8.6 *Henediella heimii* crust aside meltwater stream at Canada Glacier

Fig. 8.7 Taylor Valley, view toward Lake Fryxell (*left*), Canada Glacier (*center*), and Nussbaumriegel (*center*, above Canada Glacier)

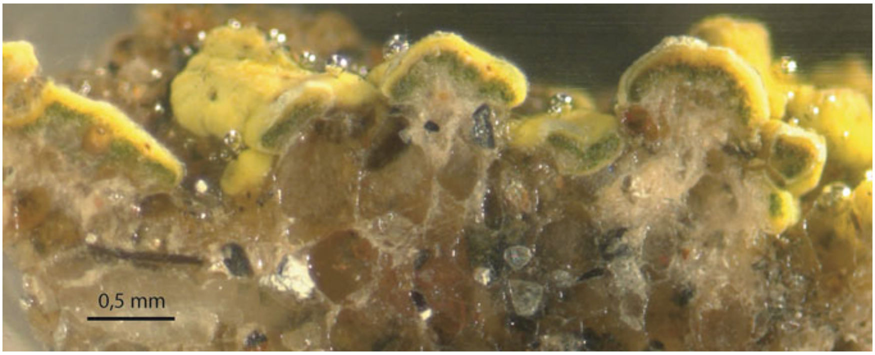


Fig. 8.8 *Acarospora gwynii*—green algal crust, cross section, showing penetration depth of rhizines (*white* felt)

Fig. 8.9 *Acarospora gwynii*, habitus of wet thallus with apothecia (*black*)

samples without identifying them to species level. Despite that, moss and lichen flora were found to be sparse with no bryophytes and only four lichens (*Lecidea cancriformis* C. W. Dodge and G. E. Baker, *B. frigida*, *Lecanora fuscobrunnea* C. W. Dodge and G. E. Baker, and *A. gwynii*) (Figs. 8.8, 8.9). The lichen *A. gwynii* was found to grow on the lower surface of sandstone, and these were also the only sites where terrestrial algae (Chlorophyta, Xanthophyceae) could be found (Magalhães et al. 2012). Continuing south to the Dufek Massif (82°S), there are no bryophytes and only a single lichen species was recorded, *Lecanora cancriformis* (Hoffm.) Vain (Hodgson et al. 2010), which is a typical epilithic lichen, and therefore cannot be considered as a biological soil crust species. Nevertheless, there are cyanobacteria and algae reportedly growing in the soils (*Oscillatoria* sp. *Trebouxia* sp. *Heterococcus* sp., Hodgson et al. 2010). In contrast to that very sparse vegetation at the Dufek Massif further south at the Queen Maud Mountains (84°S), there is a surprisingly high diversity reported (Green et al. 2011a, b). A

Fig. 8.10 *Caloplaca citrina*-dominated crust spot, Valley floor, Taylor Valley

total of 30 lichen species and 41 moss species were recorded. Most of the species were found at Ebony Ridge (83°46′S) or Mt. Harcourt (83°48′S). Four of the described species (*C. citrina*, *Caloplaca* sp., *C. flava,* and *L. expectans*) are reported to grow on mosses on the soil (Fig. 8.10). The southernmost recordings for algae, lichens, and fungi for Victoria land are by Broady and Weinstein (1998) in La Gorce Mountains (86°39′S). The authors describe the two lichen species *L. cancriformis* and *Carbonea vorticosa* (Florke) Hertel growing on a single rock face. In a fissure dissecting this rock face, they found an algal-dominated thin black mat covering not more than 10 cm^2 of a lithosol. This mat was dominated by interwoven filaments of *Hammatoidea normanni* W. Et G. S. West with associated aggregates of *Gloeocapsa* spp. and *Stichococcus bacillaris* Nägeli (Broady and Weinstein 1998). In total, 23 soil-inhabiting algae and cyanobacteria were described in this study.

8.3 Structure and Composition of Antarctic Biological Soil Crusts

Most of the studies dealing with cryptogamic organisms from continental Antarctica focus on the presence of certain organisms, their diversity, and rarely their associations or subassociations. Information is only given in a few cases if these organisms occur loosely distributed in and over the soil, or if they are organized in the form of BSCs. Except from the reports on Antarctic BSCs reviewed in this chapter, we aimed to deduce the probability of BSC presence for continental Antarctic regions from existing species lists in the referring literature. The results are summarized in a comparative list (Table 8.1) of the three major regions focused on in this study. However, especially when dealing with cyanobacteria and green algae, this is only possible if species or at least genus names are given. In such cases, one can conclude from the ecological properties assigned to taxon names their crust-forming potential.

Table 8.1 List of taxa potentially involved in soil crusts formation (mosses, lichens, green algae, cyanobacteria) in the three different continental Antarctic regions

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Mosses					
Bryoerythrophyllum recurvirostre	x			Soil	Ryan et al. (1989)
Bryum argenteum			x	Soil	Rudolph (1963)
Bryum subrotundifolium			x	Soil	Seppelt and Green (1998)
Bryum pseudotriquetrum	x	x	x	Soil	Ryan et al. (1989), Melick and Seppelt (1997), Seppelt et al. (1995)
Ceratodon purpureus	x	x	x	Soil	Ryan et al. (1989), Melick and Seppelt (1997), Seppelt and Green (1998)
Didymodon gelidus			x	Soil	Seppelt and Green (1998)
Grimmia sp.	x			Soil	Bowra et al. (1966)
Grimmia antarctici		x	x	Soil	Melick and Seppelt (1997), Seppelt and Green (1998)
Grimmia plagiopodia			x	Soil	Seppelt and Green (1998)
Grimmia lawiana	x			Soil	Kanda (1987)
Henediella heimii	x		x	Soil	Kanda et al. (2002), Seppelt and Green (1998)
Pottia austro-georgica	x			Soil	Kanda et al. (2002)
Sacrconeurum glaciale	x		x	Soil	Bowra et al. (1966), Seppelt and Green (1998)
Schistidium antarctici			x	Soil	Green et al. (2011a, b)
Schistidium urnulaceum			x	Soil	Green et al. (2011a, b)
Tortula cf. *princeps*			x	Soil	Alfinito et al. (1998)
Lichens					
Acarospora chlorophana	x			Soil, on gravel	Inoue 1995
Acarospora gwynii	x		x	Yellow crust, on soil	Bowra et al. (1966), Nienow and Friedmann (1993)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Alectoria minuscula	x			On mosses over soil	Bowra et al. (1966)
Buellia	x			On gravel	Inoue (1991)
Buellia spp.	x			Soil, on gravel	Inoue (1995)
Buellia frigida	x	x	x	Soil, on gravel	Inoue (1995), Melick and Seppelt (1997), Nienow and Friedmann (1993)
Buellia grimmiae		x		Soil	Melick and Seppelt (1997)
Buellia latemarginata	x			Soil, on gravel	Inoue (1995)
Buellia punctata	x			Soil, on gravel	Inoue (1995)
Caloplaca	x			On gravel	Inoue (1991)
*Caloplaca citrina**	x	x	x	On moss and on soil, on gravel	Inoue (1995), Melick and Seppelt (1997), Seppelt et al. (1995)
Caloplaca athallina			x	On moss	Seppelt et al. (1995)
Candelaria murrayi		x	x	On mosses and soil	Seppelt (2002), Castello and Nimis (2000)
Candelariella flava		x	x	On mosses or on soil	Melick and Seppelt (1997), Castello and Nimis (2000)
Candelariella hallettensis	x			Soil, on gravel	Inoue (1995)
Candellariella vitellina	x			On mosses over soil	Bowra et al. (1966)
Carbonea capsulata	x			Soil, on gravel	Inoue (1995)
Lecanora	x			On gravel	Inoue (1991)
Lecanora sp.	x			Yellow-green crust	Bowra et al. (1966)
Lecanora (Sect. *Placodium*) sp.	x			On mosses over soil	Bowra et al. (1966)
Lecanora expectans	x		x	On moss and on soil, on gravel	Inoue (1995), (Seppelt et al. 1995)
Lecanora cf. *fuscobrunnea*	x			Soil, on gravel	Inoue (1995)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Lecanora affin. subfusca	x			Soil, on gravel	Inoue (1995)
Lecidea andersonii	x			Soil, on gravel	Inoue (1995)
Lecidea cf. *autenboeri*	x			On mosses over soil	Bowra et al. (1966)
Lecidea blackburnii			x	On moss	Seppelt et al. (1995)
Lecidea cancriformis	x			Soil, on gravel	Inoue (1995)
Lecidella simplei	x			Soil, on gravel	Inoue (1995)
Lepraria angardiana	x			On mosses over soil	Engelskjøn (1986)
Leproloma cacuminum	x			Soil, on gravel	Inoue 1995
Physcia caesia	x		x	On mosses and soil, on gravel	Inoue (1995), Castello and Nimis (2000)
Physcia dubia			x	On mosses	Castello and Nimis (2000)
Physcia muscigena	x			On mosses over soil	Bowra et al. (1966)
Pseudephebe	x			On gravel	Inoue (1991)
Pseudephebe minuscula	x	x	x	Soil, on gravel	Inoue (1995), Melick and Seppelt (1997), Castello and Nimis (2000)
Rhizocarpon flavum	x			Soil, on gravel	Inoue (1995)
Rhizocarpon schofieldii			x	On moss	Seppelt et al. (1995)
Rhizoplaca melanophtalma	x		x	Soil, on gravel	Inoue (1995), Seppelt et al. (1995)
Rhinodina sp.	x			On mosses over soil	Bowra et al. (1966)
Rinodina olivaceobrunnea	x	x		Soil, on gravel	Inoue (1995), Melick and Seppelt (1997)
Umbilicaria aprina	x		x	Soil, on gravel	Inoue (1995), Seppelt et al. (1995)
Umbillicaria decussata	x			Soil, on gravel	Inoue (1995)
Usnea		x		Soil	Melick and Seppelt (1997)
Usnea antarctica		x		Soil	Melick and Seppelt (1997)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Usnea sphacelata	x	x		Soil, on gravel	Inoue (1995), Melick and Seppelt (1997)
Usnea sulfurea	x			On mosses over soil	Bowra et al. (1966)
Xanthomendoza borealis			x	On gravel	Seppelt et al. (2010)
Xanthoria	x			On gravel	Inoue (1991)
Xanthoria elegans	x	x	x	Yellow crust, soil	Bowra et al. (1966), Melick and Seppelt (1997), Castello and Nimis (2000)
Xanthoria mawsonii		x	x	On mosses and soil	Melick and Seppelt (1997), Castello and Nimis (2000)
Green algae					
Actinotaenium	x			Soil	Broady (1986)
Actinotaenium cucurbita	x		x	On mosses and soil	Pankow et al. (1991), Alfinito et al. (1998)
Actinotaenium cucurbita var. *attenuatum*	x			On mosses and soil	Pankow et al. (1991)
Actinotaenium cucurbita rotundatum	x			On mosses and soil	Pankow et al. (1991)
Apatococcus cf. *Lobatus*			x	Soil	Cavacini (2001)
Binuclearia tectorum			x	On mosses	Alfinito et al. (1998)
Bracteacoccus	x			Soil	Broady (1986)
Carteria	x			Soil	Broady (1986)
Characium	x			Soil	Broady (1986)
Chlamidopodium starrii			x	Soil	Cavacini (2001)
Chlamidopodium			x	Soil	Cavacini (2001)
Chlamydomonas	x			Soil	Broady (1986)
Chlorella			x	Soil	Cavacini (2001)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Chlorella homosphaera	x			Soil	Broady (1986)
Chlorella saccharophila			x	Soil	Cavacini 2001
Chlorella vulgaris			x	Soil	Cavacini (2001)
Chlorococcum	x		x	Soil	Broady (1986), Cavacini (2001)
Chlorococcum cf. *elkhartiense*			x	Soil	Broady and Weinstein (1998)
Chlorosarcina	x			Soil	Broady (1986)
Chlorosphaera	x			Soil	Broady (1986)
Chloroshaera kerguelensis			x	On mosses	Alfinito et al. (1998)
Choricystis chodatti			x	Soil	Cavacini (2001)
Choricystis guttula			x	Soil	Cavacini (2001)
Coccomyxa gloeobotrydiformis			x	Soil	Cavacini (2001)
Coenochloria sp.			x	Soil	Broady and Weinstein (1998)
Cylindrocystis brebissonii	x			On mosses and soil	Pankow et al. (1991)
Cylindrcystis crassa	x			On mosses and soil	Pankow et al. (1991)
Desmococcus olivaceus		x		Soil crust	Seppelt (2002)
Diplosphaera muscosa				soil	Cavacini (2001)
Dictyosphaerium	x			soil	Broady (1986)
Gloeocystis vesiculosa			x	Soil	Cavacini (2001)
Heterotetracystis akinetos			x	Soil	Cavacini (2001)
Kentrosphaera	x			Soil	Broady (1986)
Kentrosphaera facciolae			x	On mosses and on soil	Cavacini (2001), Alfinito et al. (1998)
Klebsormidium	x			Soil	Broady (1986)
Klebsormidium montanum			x	Soil	Cavacini (2001)
Macrochloris	x			Soil	Broady (1986)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Oocystis	x			Soil	Broady (1986)
Planktosphaerella terrestris			x	Soil	Cavacini (2001)
Pleurastrum insigne			x	Soil	Cavacini (2001)
Pleurococcus antarcticus			x	Soil	Cavacini (2001)
Prasiococcus calcarius	x	x	x	Soil, soil crust	Broady (1983), Seppelt (2002), Broady (2005)
Prasiola crispa	x	x	x	Soil, soil crust	Kanda et al. (2002), Seppelt (2002), Cavacini (2001)
Pseudococcomyxa simplex			x	Soil	Cavacini (2001)
Pseudotraspora gainii			x	On mosses	Alfinito et al. (1998)
Raphidenema	x			Soil	Broady (1986)
Raphidonema pyrenoidifera			x	Soil	Cavacini (2001)
Raphidonema sempervirens			x	Soil	Cavacini (2001)
Scottiellopsis oocystiformis			x	Soil	Cavacini (2001)
Scotiellopsis terrestris			x	Soil	Cavacini (2001)
Sphaerocystis oleifera			x	Soil	Cavacini (2001)
Stichococcus	x			Soil, on moss	Broady (1986), Engelskjøn (1986)
Stichococcus bacillaris			x	On mosses and on soil	Cavacini (2001), Alfinito et al. (1998)
Stichococcus cf. *Chlrelloides*			x	Soil	Cavacini (2001)
Stichococcus mirabilis			x	Soil	Cavacini (2001)
Tetracystis	x			Soil	Broady (1986)
Tetracystis cf. *fissurata*			x	Soil	Broady and Weinstein (1998)
Cyanobacteria					
Anabaena	x			Soil	Broady (1986)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Aphanothece	x			Soil	Broady (1986)
Aphanocapsa	x			Soil	Broady (1986)
Aphanocapsa montana			x	On mosses	Alfinito et al. (1998)
Aphanocapsa parasitica			x	Soil	Cavacini (2001)
Aphanothece saxicola			x	Soil	Cavacini (2001)
Borzia tricularis			x	On mosses	Alfinito et al. (1998)
Calothrix braunii	x		x	On mosses and on soil	Pankow et al. (1991), Cavacini (2001), Alfinito et al. (1998)
Calotrix parietina	x	x	x	On moss and soil	Pankow et al. (1991), Broady (1996), Cavacini (2001)
Chondrocystis dermochroa			x	Soil	Cavacini (2001)
Chroococcus	x	x		On moss, soil crust	Engelskjøn (1986), Ling and Seppelt (1998)
Chroococcus coharens			x	On moss	Alfinito et al. (1998)
Chroococcus minutus	x		x	On moss	Pankow et al. (1991), Cavacini (2001)
Chroococcus turgidus	x		x	On moss	Pankow et al. (1991), Alfinito et al. (1998)
Crinalium	x			soil	Broady (1986)
Crinalium cf. *magnum*			x	soil crust	Broady (2005)
Cyanobacterium cedrorum			x	Soil	Cavacini (2001)
Cynosarcina cf spectabilis				Soil	Cavacini (2001)
Cyanosarcina chroococcoides			x	On moss	Alfinito et al. (1998)
Cyanothece aeruginosa	x		x	Soil, soil crust	Pankow et al. (1991), Broady (2005)
Cyanothece maior	x			On moss	Pankow et al. (1991)
Eucapsis minor			x	Soil	Cavacini (2001)
Eucapsis minuta			x	Soil	Cavacini (2001)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Gloeocapsa	x	x		Soil crust	Broady (1986), Ling and Seppelt (1998)
Gloeocapsa cf. *kuetzingianum*			x	Soil crust	Broady (2005)
Gloeocapsa dermochroa			x	On mosses	Alfinito et al. (1998)
Gloeocapsa ralfsiana			x	On mosses	Alfinito et al. (1998)
Gloeothece	x			Soil	Broady (1986)
Hammatoidea normanni			x	Soil	Broady and Weinstein (1998)
Katagnymene		x		Soil	Ling and Seppelt (1998)
Katagnymene accurata	x			On moss and soil	Pankow et al. (1991)
Komvophoron schmidlei			x	On moss	Alfinito et al. (1998)
Leptolyngbya foveolarum			x	Soil	Cavacini (2001)
Leptolyngbya frigida			x	On moss and soil	Alfinito et al. (1998)
Lyngbya	x			Soil	Broady (1986)
Lyngbya aerugineo-coerulea	x			Soil	Pankow et al. (1991)
Lyngbya fritschii	x			On moss and soil	Pankow et al. (1991)
Lyngbya scotti			x	Soil	Cavacini (2001)
Microcoleus vaginatus	x		x	Soil, soil crust	Pankow et al. (1991), Broady (2005)
Microcystis parasitica			x	On moss	Alfinito et al. (1998)
Nodularia harveyana		x	x	On mosses and on soil	Broady (1996), Cavacini (2001)
Nostoc	x			Soil	Broady 1986
Nostoc commune	x		x	On moss and soil	Kanda et al. (2002), Cavacini (2001)
Nostoc punctiforme			x	Soil	Cavacini (2001)
Oscillatoria	x			Soil	Broady (1986)
Oscillatoria chlorina	x			Soil	Pankow et al. (1991)
Oscillatoria irrigua	x			Soil	Pankow et al. (1991)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Oscillatoria simplicissima var. *antarctica*			x	On mosses	Alfinito et al. (1998)
Phormidium	x			Soil	Broady (1986)
Phormidium aerugineo-coeruleum			x	On mosses	Alfinito et al. (1998)
Phormidium animale			x	On mosses	Alfinito et al. (1998)
Phormidium attenuatum			x	Soil	Cavacini (2001)
Phormidium autumnale	x		x	On moss and soil	Pankow et al. (1991), Broady and Weinstein (1998)
Phormidium corium			x	Soil	Cavacini (2001)
Phormidium foveolarum			x	On mosses	Alfinito et al. (1998)
Phormidium frigidum			x	On mosses	Alfinito et al. (1998)
Phormidium priestleyi			x	Soil	Cavacini (2001)
Phormidium productum			x	On mosses	Alfinito et al. (1998)
Phormidium pseudopriestley			x	Soil	Cavacini (2001)
Phormidium uncinatum			x	Soil	Cavacini (2001)
Rhabdoderma sigmoidea			x	On mosses	Alfinito et al. (1998)
Scytonema schmidtii			x	Soil	Cavacini (2001)
Scytonema myochrous		x			Broady (1996)
Scytonema velutinum	x			Soil	Pankow et al. (1991)
Stigonema	x	x		Soil, soil crust	Broady (1986), Ling and Seppelt (1998)
Stigonema minutum	x			Soil	Pankow et al. (1991)
Stigonema ocellatum	x			Soil	Pankow et al. (1991)
Synechococcus	x	x		Soil, soil crust	Broady (1986), Ling and Seppelt (1998)

(continued)

Table 8.1 (continued)

Taxa	Region			Habitat, remarks	Source
	Dronning Maud Land	Wilkes Land	Victoria Land		
Synechococcus maior			x	On mosses	Alfinito et al. (1998)
Synechocystis	x			Soil	Broady (1986)
Tolypotrix	x			Soil	Broady (1986)
Tolypothrix tenius		x		Soil	Broady (1996)

**Note added in proof* according to Søchting and Castello (2012), in contrast to many reports, the species *Caloplaca citrina* is not confirmed for Antarctica anymore. Species assigned to *Caloplaca citrina* from Antarctica refer to either *Caloplaca darbishirei* or *Caloplaca soropelta*

Biological crust formation depends on the capability of cyanobacteria or algae to produce large amounts of extracellular polysaccharide substances (EPS) in the form of sheaths gluing soil particles to form stable crusts (Belnap and Lange 2003). Where only operational taxonomic units (OTUs) are presented without linking them to described taxa, nothing can be concluded about the ecology of these organisms, except the presence of cyanobacteria on higher taxonomic ranks such as orders. Apparently, common crust-forming cyanobacteria are very rare in Antarctica (see Table 8.1). For example, the genus *Microcoleus* was only found twice and with one species only (Schirmacheroasis; Pankow et al. 1991 and Victoria Land; Broady 2005). This might be one of the reasons why cyanobacterial crusts, common in hot deserts and semi-deserts (see for example Pointing and Belnap 2012), are rare in continental Antarctica.

8.3.1 Cyanobacterial BSC

Polar BSC consist of surface soil aggregates held together by cyanobacteria and algae (Fletcher and Martin 1948; Campbell et al. 1989). Pankow et al. (1991) explicitly mention cyanobacterial crusts from the Schirrmacheroasis, as well as Ling and Seppelt (1998) from the Windmill Islands. The two latter BSCs are so far the only ones, where the typical filamentous cyanobacterium *Microcoleus vaginatus* was found. *M. vaginatus* is the most common BSC cyanobacterium worldwide and is well known to initiate crust formation with their long filaments having a sticky sheath and containing thousands of trichomes. The filaments can become several millimeters, sometimes even centimeters long and live in the upper centimeter of soil. Later on, other unicellular and filamentous cyanobacteria and algae may associate. The final stage may include bryophyte and lichen species as well (Pankow et al. 1991).

Whether or not the *N. commune* Vaucher covered areas, common within the boundary crevices of frost sorted polygons, may be considered BSCs is not easy to decide. BSC are cyanobacteria, algae, bryophytes, fungi, and lichens living either singularly or in different proportions in the upper few millimeters of soil or whose life cycle is at least partly inside the soil (Belnap and Lange 2003). Most of their lifetime, the large gelatinous and poikilohydric colonies of *N. commune* are lying on the ground and dry colonies can easily be blown and spread by the wind. Only a short period of the life cycle takes place inside the soil. These are the stages of singular mobile trichomes and colony primordia, developing into macroscopic colonies on the soil surface. Depending on environmental conditions, these cryptic developmental stages in the soil last for a few hours or days (Mollenhauer 1986).

Most *Nostoc* samples that were either collected moss associated, free living on moist soil, or from flat ponds in Victoria Land were found to belong to the species *N. commune* (Novis and Smissen 2006). This study also showed that *N. commune* from Antarctica is separated into two different clusters, one cluster containing all *N. commune* populations from soil and the second including those from ponds.

8.3.2 Green Algal BSC

Soil crusts dominated by green algae like *P. crispa*, *P. calcarius,* and *Desmococcus olivaceus* (Persoon ex Acharius) J.R. Laundon occur at eutrophic sites, for example, in the surroundings of penguin rockeries (Seppelt 2002). While *P. crispa* with its macroscopic filmy thalli spreads on the soil surface, the other two species can also be found inside the upper few millimeters of the soil (Fig. 8.11a).

8.3.3 Bryophyte–Cyanobacteria BSC

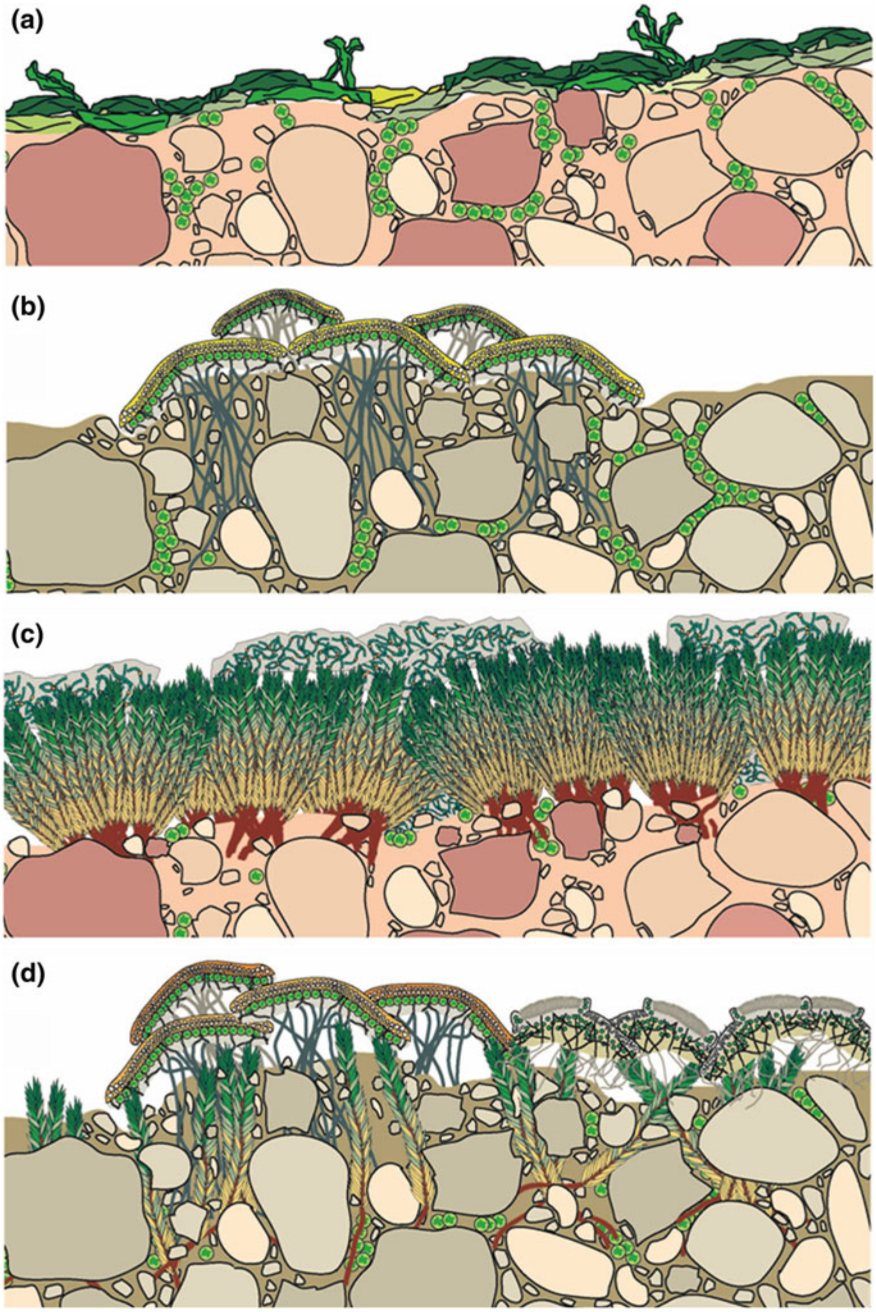
Bryophyte carpets along the meltwater flushes of glaciers are the most conspicuous crust types of continental Antarctica (Green and Broady 2001). The bryophytes emerge from the upper few centimeters of soil and cover the surface with spherical cushions (Figs. 8.11c, 8.12, 8.13). The moss cushions are very often associated with macroscopic colonies of *N. commune*, attached to the surface of moss cushions (Figs. 8.11c and 8.14), and with microscopic thalli of filamentous cyanobacteria such as *Tolypothrix*, *Calothrix,* and *Leptolyngbya* (own observations, unpubl.).

8.3.4 Bryophyte–lichen BSC

BSC dominated by bryophytes and lichens being associated with cyanobacteria and green algae are typical features in areas with a higher vegetation cover. Eighteen out of 51 lichen species (Table 8.1) are described to grow on soils in Antarctica, are also described to grow on mosses. Growing on top of mosses (Figs. 8.11d, 8.15) may provide advantages for the lichens (Colesie et al. 2011). Having a five times deeper soil penetration depth compared to the above ground layer (Colesie et al. 2013), this crust type has significant soil-stabilizing relevance.

8.3.5 Lichen–Green Algal BSC

This peculiar type of BSC was described only once from the Diamond Hill region (Fig. 8.16). The dominating lichen species is *A. gwynii* C. W. Dodge and E. D. Rudolph, penetrating deep into the soil, accompanied by the green algae *Diplosphaera*, *Heterococcus*, and *Trebouxia* sp. (Fig. 8.11b). Neither mosses nor cyanobacteria were associated with these crusts. The lichen rhizines adhere to soil particles, building compact soil aggregations. Bowra et al. (1966) described lichens (*Xanthoria*, *Lecanora,* and *Acarospora chlorophana*) as yellow or yellow-green crusts but did not mention associations with other soil crust-forming organisms.


(a)
(b)
(c)
(d)

◀ **Fig. 8.11** Schemes of typical Antarctic biological soil crusts. **a** *P. crispa*—green algae crust. Foliose *P. crispa* on top of soil, unicellular green algae inside the soil. **b** Lichen—green algae crust. Unicellular green algae inside the soil, lichens on top with rhizines penetrating deep into the soil. **c** Bryophyte—cyanobacterial crust, bryophyte cushions on top with their rhizoids penetrating the soil; cyanobacterial colonies (*Nostoc*) on top of moss cushions, small cyanobacterial colonies inside the cushions between leaflets of mosses. **d** Bryophyte—lichen crust; bryophytes embedded in the soil, only the upper part reaches the top soil layer, lichens grow on top of the mosses, and unicellular green algae grow inside the soil

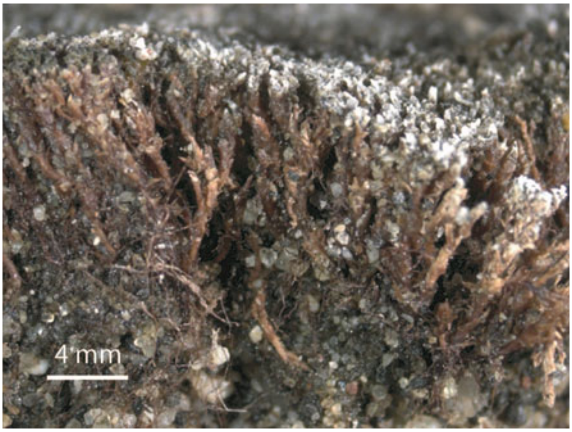


Fig. 8.12 Bryophyte crust, cross-fracture, *Henediella heimii* with frost damage on *top* of the stems

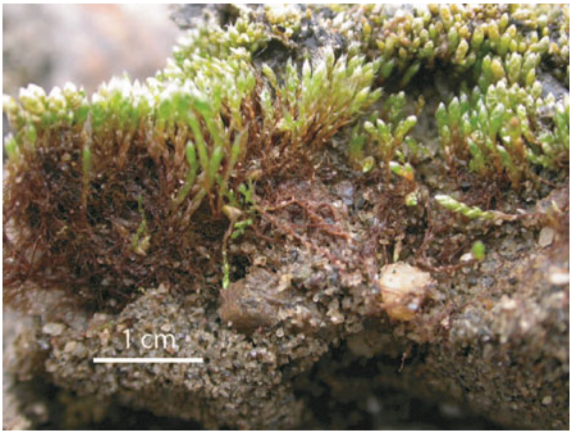


Fig. 8.13 *Henediella heimii* from a bryophyte flush aside a meltwater stream

Fig. 8.14 *Nostoc commune*, young gelatinous colony from a bryophyte flush

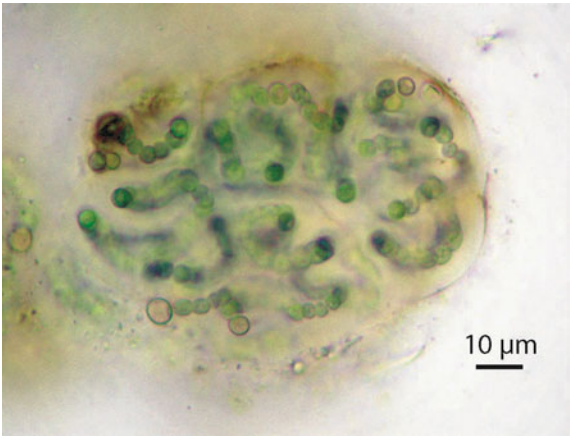


Fig. 8.15 Cross-fracture through bryophyte—lichen crust; from top to bottom: *Lecanora expectans*, *Henediella heimii* (*brown* stems)

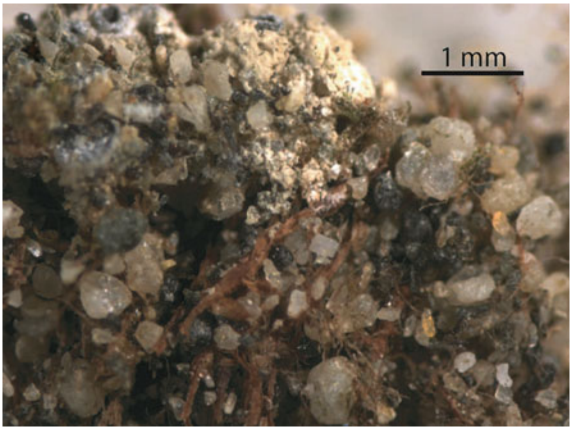


Fig. 8.16 *Acarocpora gwynii*—green algal crust at Diamond Hill, Darwin Glacier region

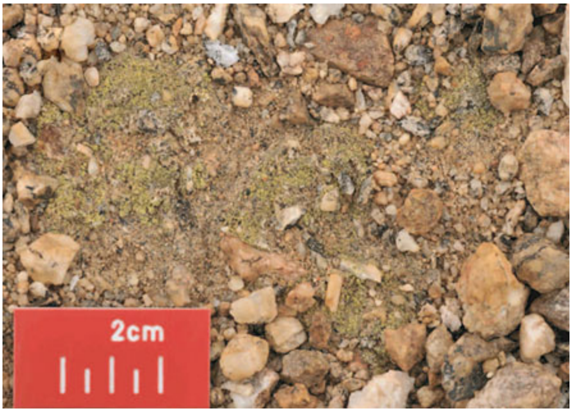


Table 8.2 Examples for culture-independent nominations of cyanobacteria from Victoria Land soils

"Taxon" or other category	Attribution and location	Method	Source
Ribo-type, closest cultured relative *Leptolyngbya* sp. PCC9207	Microbial mat, Lake Fryxell	Restriction fragment length polymorphisms (RFLP)	Aislabie et al. (2006)
Several OTUs of Nostocales; Oscillatoriales, Chroococcales, Gloeobacteriales	Terrestrial mat at the edge of larger rocks and boundary crevices of frost polygons	Clone library, DGGE + band sequencing,	
isolation + sequencing	Hodgson et al. (2010)		
68 ARISA AFLS of cyanobacteria (no information on OTUs or taxa)	Soil, surroundings of Lake Wellman, Darwin Glacier region	ARISA-AFLS ITS	Magalhães et al. (2012)
Nearest matches: *Acaryochloris* sp., *Nostoc* sp., *N. calcicola*, *N. edaphicum*, *Phormidium priestleyi*, *Phormidium murrayi*, *Chroococcidiopsis* sp., *Leptolyngbya* sp., and *Leptolyngbya antarctica*, most of them with more than 80 % safety	Edaphic cyanobacteria, Dry Valleys, Miers, and Beacon Valley	ARISA-AFLS; 16S rDNA	Wood et al. (2008)
17 OTUs, 23.5 % *Chroococcales*, 58.8 % *Oscillatoriales* (*Leptolyngbya*, Phormidium), 5.9 % Nostocales (Nostoc)	Soil, Taylor Valley	Clone libraries of 16S rDNA	Michaud et al. (2012)
Cyanobacteria, *Oscillatoriales,* no quantification	High-productivity soils, Admiralty range, Northern Victoria Land	RFLP, DGGE, 16S rRNA	Niederberger et al. (2008)

8.4 Conclusions

The concept of BSC is apparently not established in the research of Antarctic terrestrial ecology. It is very common to determine and list the organismic diversity of Antarctic soils, without taking into consideration whether the organisms found might form a specific association or even biocoenosis.

The comparison of results on organism composition of terrestrial photoautotrophic communities, obtained by the exclusive use of expert knowledge with those derived from exclusive molecular techniques, shows that neither method produces reliable results. While studies based on morphology and culture techniques work well in detecting the major species, they may often fail to get the total species diversity. However, molecular studies are often based on different and thus hardly comparable methods, resulting in different categories of organisms (Table 8.2) that can hardly be used to draw ecological conclusions from them.

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Chapter 9
Lithobionts: Cryptic and Refuge Niches

Thulani P. Makhalanyane, Stephen B. Pointing and Don A. Cowan

Abstract Lithic-associated microhabitats, referred to as lithobiontic ecological niches and their communities are termed lithobionts. Lithic niches are widely dispersed in Antarctica and allow microbial communities to circumvent environmental stressors such as temperature fluctuations, low moisture levels, and high ultraviolet radiation. Here, we assess the status of research on the three recognized classes of lithobiont communities (epiliths, hypoliths and endoliths). We describe the microbial diversity of lithobionts, the factors that influence colonization, and the roles played by these communities in the Antarctic soil ecosystem. In order to understand community dynamics, such as beta-diversity patterns and factors that drive them, we advocate the application of "omics-based approaches" that can reveal both the functional capacities and adaptive potentials of complex microbial communities.

9.1 Introduction

The ice-free polar desert landscapes of Antarctica present an extremely challenging environment for life. Severe thermal, moisture and UV stress is exacerbated by an ultraoligotrophic terrestrial landscape that is comprised largely of mineral soils and rocks (Cary et al. 2010). Higher plants and animals are absent

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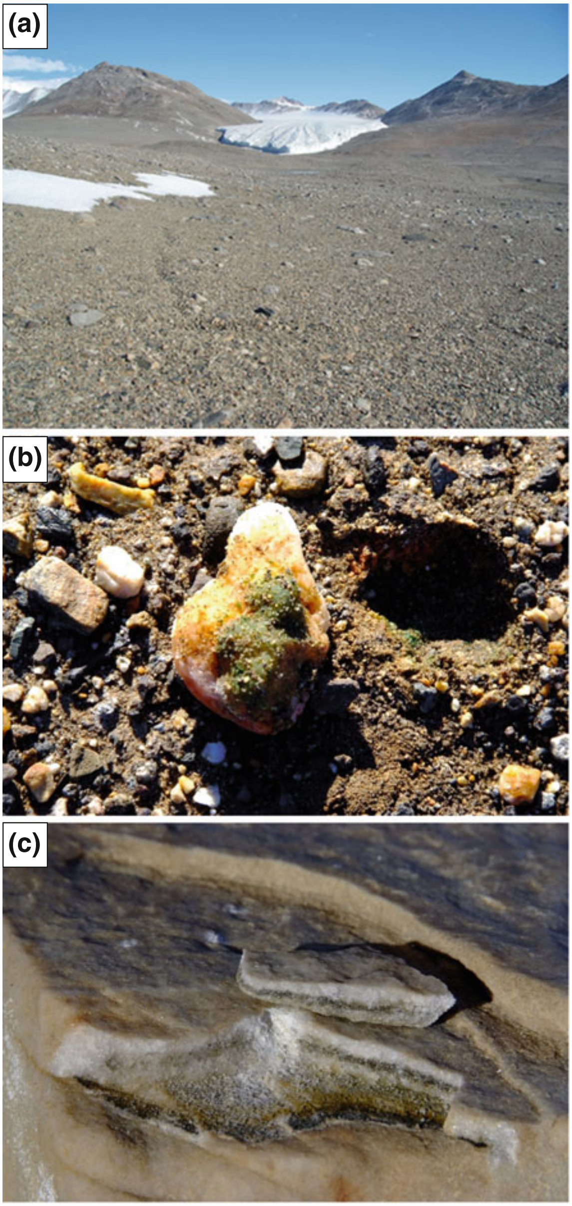
Fig. 9.1 Microbial colonization in hyperarid deserts. **a** Landscape of Miers Valleys, Antarctica illustrating a desert pavement covered with rocks supporting the development of **b** hypolith and **c** endolith communities (Photograph credits: Don A. Cowan)



from this environment, and instead, the biotic component of this ecosystem is almost exclusively microbial (Cowan and Tow 2004). The largest and best understood of the ice-free regions is the McMurdo Dry Valleys (Fig. 9.1), and this hyperarid desert supports vast expanses of exposed rocky substrate. Microbial colonization of various rock substrates occurs, although this is cryptic and not

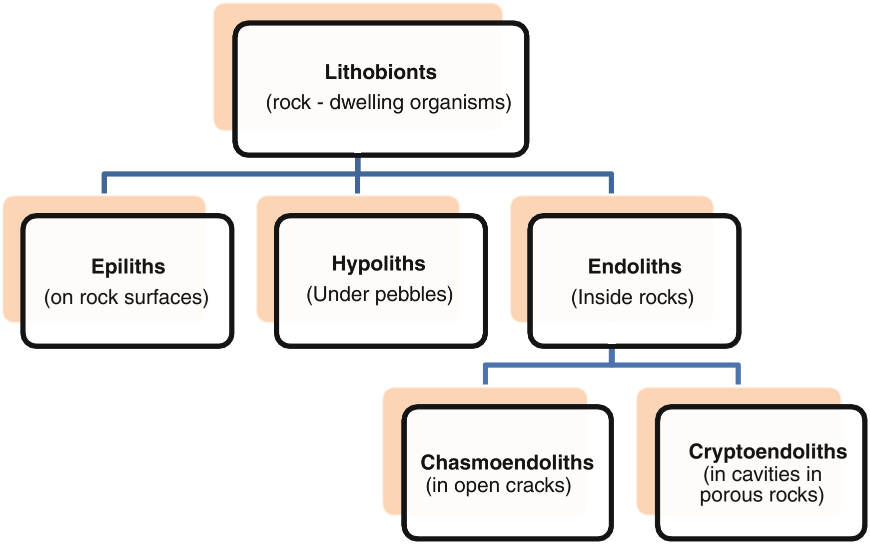


Fig. 9.2 Classification of lithobiont niches inhabited by desert microorganisms

readily observed on many surfaces. These lithic-associated microhabitats are referred to as lithobiontic ecological niches, and their communities are termed lithobionts (Golubic et al. 1981). Numerous studies have shown that lithobionts [also referred to as soil rock surface communities (SRSCs)] are widespread in both hot and cold deserts and are often the only visible life in such extreme terrestrial environments (Pointing and Belnap 2012). These communities are thought to contribute significantly to the ecology and function of both hot and cold deserts.

In this chapter, we review the status of research on the three recognized classes of lithobiont communities (Fig. 9.2): epiliths adhere to the surface of the rock, endoliths are found within the rock matrix, and hypoliths attach to ventral rock surfaces. We describe the microbial diversity of lithobionts, factors that influence colonization and the role played by these communities in the Antarctic ecosystem.

9.2 Lithobiontic Ecological Niche

The three lithobiontic niches are delineated largely as a function of the mineral substrate. Epiliths are perhaps the least fastidious and occur on various igneous rock surfaces. Endolithic colonization is restricted to porous sandstones and weathered granitic rocks, while hypoliths generally develop beneath translucent quartz and marble rocks (Pointing and Belnap 2012). Examples of epilithic, endolithic and hypolithic colonization are shown in Fig. 9.1.

9.2.1 Epiliths

Epilithic organisms populate the surfaces of stable rock substrata with access to sufficient quantities of moisture (Wynn-Williams 2002; Smith 1982). The establishment of epiliths is often associated with moss and lichen communities on the rock surfaces (Pointing and Belnap 2012; Nash et al. 1977), although heterotrophic fungi and cyanobacteria also appear to be key constituents (Staley et al. 1982; Gorbushina 2007).

Epilithic colonization is perhaps the most vulnerable of the three lithic types, as they are exposed to strong winds, ultraviolet radiation (UVR), desiccation and other perturbations (Cockell et al. 2008; Wynn-Williams and Edwards 2000). As a consequence, epiliths are often restricted to the milder lower latitude Antarctic regions such as Princess Elizabeth Land and Mac Robertson Land (Broady 1981a, 1996; Wynn-Williams and Edwards 2000).

9.2.2 Endoliths

Endolithic microbial communities colonize the interior of rocks by adapting to the different ecological sub-niches within the lithic substrate (Golubic et al. 1981). Depending on the micromorphological and structural properties of the rock, endoliths can be found as interstitial habitats of cracks and fissures (chasmoendoliths or chasmoliths) and also in pore spaces between mineral grains (cryptoendolithic) (Golubic et al. 1981; Nienow and Friedmann 1993; Budel et al. 2009). Chasmoliths are commonly found in siliceous rocks, but also have been reported in granite, marble, silicified sandstone, gypsum crusts and anorthosite (Friedmann 1982; Broady 1981b; de los Rios et al. 2005b). In contrast, cryptoendoliths are principally associated with porous sandstone rocks (Bell 1993; Friedmann and Ocampo-Friedmann 1984; Nienow et al. 2003; Omelon 2008; Sun et al. 2010), but may also be recovered in other suitable mineral types including granite, gneiss, limestone, marble, gypsum, halite and evaporites (Cockell et al. 2002; Nienow and Friedmann 1993; Boison et al. 2004; Wierzchos et al. 2006).

It has been demonstrated that cryptoendolithic microbial communities in Beacon sandstones, in the Antarctic Dry Valleys, promote biogenic weathering of rock substrates, and colonized sandstones show distinct exfoliation patterns on the rock surface (Friedmann and Weed 1987; Nienow and Friedmann 1993). Colonized sandstones display different coloured patches (white, yellow, orange or brown), the result of both the constructive aeolian weathering process and the destructive biogenic weathering process (Sun and Friedmann 1999; Sun et al. 2010). Long-term microbial colonization and the biogenic accumulation of oxalic acid dissolve the cementing substances between the mineral grains, resulting in exfoliation of the surface crust and loss of biomass (Sun and Friedmann 1999). This exfoliative weathering process is cyclic, and each phase is estimated to last for 1×10^4 years

(Friedmann et al. 1993; Sun et al. 2010). The process contributes to both the formation of mineral soils and the organic carbon fraction in the soil phase (Nienow and Friedmann 1993).

Chasmoliths are found in both the vertical fissures and horizontal cracks in rocks; the former are common in quartz glacial debris, whereas the latter are common in charnockite (a rare type of granite containing pyroxene) substrates (Vincent 2004). They are also frequently described in the fine fracture zones of marble which is common to the Antarctica landscape (Vincent 2004; Cowan and Ah Tow 2004). Chasmoliths are not exclusive to Antarctica, and they have been reported from other deserts in central Asia, central Australia, south-western USA and Mexico (Broady 1981b; Friedmann et al. 1967; Friedmann and Ocampo-Friedmann 1984).

9.2.3 Hypoliths

Hypolithic microbial communities (hypolithons) inhabit the ventral surfaces of rock substrates at the rock–soil interface (Friedmann et al. 1967; Golubic et al. 1981). Hypolithons typically colonize translucent rocks such as quartz, gypsum and granite (Broady 1981a, b) but may also be found under opaque rocks (e.g. dolomite and gneisses) (Cockell and Stokes 2004, 2006). As with endoliths, hypolithic communities are dominated by photoautotrophs such as cyanobacteria, which require a minimum level of photosynthetically active radiation (PAR) for photosynthesis (discussed below) (Friedmann et al. 1993).

In an observational study, three types of hypolithic communities were reported in the Miers Valley: the cyanobacterial dominated (Type I), the fungal dominated (Type II) and the bryophyte dominated (Type III) (Cowan et al. 2011a, b). The morphological characteristics of growth in these communities differ, and the hypolithons may be either loosely attached to the rock or unattached depending on the main community components. Type I hypoliths adhere directly to the rock forming a biofilm composed primarily of filamentous oscillatorian cyanobacterial morphotypes (Pointing et al. 2009). Type II communities comprise a filamentous network structure cemented to the rock surface, while the macroscopic moss structures of Type III communities are embedded in the soil under the translucent rock (Cowan et al. 2010a). These hypolithic types are both morphologically complex and diverse in composition. The community structures of hypolithic communities has recently been determined using amplified RNA intervening sequence analysis (ARISA), terminal restriction fragment length polymorphism (T-RFLP), clone library construction and pyrosequencing analysis of the 16S rRNA gene phylogenetic market gene (Wood et al. 2008; Pointing et al. 2009; Cowan et al. 2011a, b; Makhalanyane et al. 2013a).

9.3 Establishment of Lithobiontic Communities

Lithic communities have been described associated with a variety of substrates, including fine-grained Beacon sandstone, limestone, gypsum and flint (Nienow and Friedmann 1993; Cowan et al. 2010c; Cary et al. 2010; Cockell and Stokes 2004). Colonization of the rock is thought to depend on a combination of abiotic factors including macro- and microclimate (discussed below), ultrastructure, mineral composition and pH, which together contribute to the ability of the rock to host microorganisms (Friedmann and Ocampo-Friedmann 1984). Biotic factors are also involved during the colonization process. For instance, cyanobacteria are known to dominate habitats with high pH values and high levels of calcium and magnesium carbonates (Johnston and Vestal 1989). Fungal-dominated habitats have been reported from high altitude locations with high metal oxide concentrations (Connell et al. 2006; Pointing et al. 2009).

9.3.1 *Temperature*

The temperature of the lithobionts has been found to be closely linked to the ambient air temperature and the level of solar radiation (Nienow and Friedmann 1993). However, thermal buffering, due to the black body absorption effect of opaque rocks or the "greenhouse effect" of translucent quartz rocks, has been detected (Friedmann 1980; McKay et al. 2003; Schlesinger et al. 2003; Wynn-Williams 2002; Cowan et al. 2011a, 2010c). Daytime peak rock-air temperature differences in the Antarctic Ross Desert and in the Sonoran Desert in North America were 15 and 10 °C, respectively, indicating similar trends for both hot and cold deserts (Friedmann 1980; McKay and Friedmann 1985). However, three recent studies (Azua-Bustos et al. 2011; Makhalanyane et al. 2013b; Tracy et al. 2010) measuring microclimatic variables in hypolithons from hot deserts reported lower temperatures at the rock surface interface in daytime and night-time, and warmer night-time temperatures when compared to open soil in conflict with earlier studies (Schlesinger et al. 2003).

Depending on a number of factors including aspect, elevation and other geographical features, the annual temperatures in the McMurdo Dry Valleys ranges from −14.8 to 30 °C, with differences between the maximum and minimum of approximately 50 °C (Doran et al. 2002). These extreme temperature ranges impose severe freeze–thaw stresses on microorganisms (Nienow et al. 1988). Therefore, it has been hypothesized that the thermal buffering provided by rocks is perhaps most significant in polar deserts as lithobionts are protected from rapid freeze–thaw stress (Wynn-Williams 2002; Cowan et al. 2010c, 2011a). The effect of katabatic wind episodes, which have a direct effect on both temperature fluctuations and the physical stability of soil crusts, is also minimized by the lithobiontic lifestyle. Reports suggest that surface rock temperature can be up to 20 °C higher than ambient air temperatures during sunny periods (Kappen et al. 1983). The warmer rock mass may also prolong the period of lithophytic microbial growth in polar deserts during polar summers (Wynn-Williams 2002).

9.3.2 Water Availability

The rock microhabitat has been shown to offer improved water availability compared to the surrounding soil (Tracy et al. 2010; Cowan et al. 2010c; Chan et al. 2012; Warren-Rhodes et al. 2006). In rainfall zones (such as the Antarctic Peninsula), the overlying rock provides protection from raindrop impact during precipitation, but provides a narrow annuli of unsealed soil near the sheltered margins of stones, that serve as sites for water entry and air escape for lithic niches (Thomas 1997). The rock also serves as a collector of water during precipitation, fog and dew events (Warren-Rhodes et al. 2006).

Liquid water is an essential requirement for the development of epilithic colonists. Increases in precipitation have been reported to lead to surges in cover and biomass (Broady 1996, 1989). As a result, epilithic colonization is highest at moist coastal areas and locations with frequent irrigation by snowmelt or high atmospheric humidity, and around bases of nunataks where exposed rocks meet surrounding ice fields (Broady 1981b, 1989, 1996). The diversity of Antarctic epiliths has been reported to drop significantly along moisture gradients. For example, the total lichen species diversity was found to decrease from 18 genera in Dronning Maud Land (approximately 200 km inland) to only 5 genera a further 1,000 km from the coast in the Pensacola Mountains (Cameron 1972; Engelskjøn 1986; Wynn-Williams 2002).

Hypolithons access water from rainwater runoff collected and from condensation on the rock surface during fog and dew events (Bullard 1997; Warren-Rhodes et al. 2006). The overlying rock also serves as a physical impediment to evaporation (Wynn-Williams 2002). The water content of Dry Valleys soils below hypolithon-colonized rocks has been shown to range from 6 to 14 % w/w, with open soils containing significantly less moisture (0.5–2 % w/w) (Smith et al. 2000). Other factors, such as porosity of the rock, have also been shown to help retain moisture (see below) (Friedmann 1980; Kappen et al. 1983).

Water availability in soil has been shown to regulate the upper boundary for growth, while the lower boundary is determined by the light regime, controlled by the translucence of the overlying rock substrate. In Antarctic hypoliths, quartz rocks have been reported to effectively filter UVA and UVB radiation, both potentially detrimental to colonization (Cowan et al. 2010c). Moisture also improves light transmittance through the rock, because light scattering is reduced when all air spaces between mineral particles are filled with water (Vincent 2004).

Extracellular polymeric substances (EPS) have been described for several lithobiontic communities (de los Ríos et al. 2003, 2005a; Pointing and Belnap 2012). The role of EPS is thought to be essential in terms of water relations in lithobionts. Both composition and hygroscopic properties provide a matrix for water absorption and retention and for absorbing organic compounds and ions. de los Rios et al. (2004) have speculated that EPS may be essential both for preserving the microbial populations in lithobionts and for facilitating photosynthesis in endolithic cyanobacteria. Microbial EPS can also promote soil fertility, as the components of the matrix create a mosaic of polyfunctional binding sites that retain excess heavy metals while concentrating growth-promoting nutrients on the sheath (Gadd 1990). The collection and absorption of dew by hypolithons have been quantitatively correlated with EPS abundance (Gorbushina 2007).

9.3.3 Light Availability

The translucence of the rock substrate is critical for refuge lithobiont colonization and growth. Although light transmission through the quartz pebbles of 13–80-mm thickness was filtered to 0.9–2.7 % of the incident sunlight (Broady 1981b), the presence of cyanobacterial-dominated microbial communities is tangible evidence that such low light levels are sufficient to support photoautotrophic processes. Porosity and translucence of the rock substrate are the most important properties which enable colonization in endoliths (Cowan and Ah Tow 2004). The interior surfaces of the rock are characterized by a steep light gradient along depth due to light attenuation by rock substrates (Friedmann 1980). The porosity of rocks ranges from 0 to 50 % and is influenced by many factors such as rock type, the mineral content and grain particle size (Šperl and Trčková 2008).

In the polar regions, it has been reported that the hypolithic colonization of opaque rocks was promoted by local periglacial activities (the freezing and thawing of ground water) which sort rocks and stones into polygonal spatial arrangements, creating openings around the margins of quartz rocks and facilitating the penetration of light to the undersides (Cockell et al. 2002; Cockell and Stokes 2004). The attenuation of light by rocks also assists microbial colonization by effectively reducing UVR stress in refuge lithic niches (Broady 1981b; Cowan et al. 2010c; Wong et al. 2010a).

The extent of light penetration through different rock substrates has been found to determine the abundance of hypolithic colonizations under translucent and opaque rocks (Berner and Evenari 1978). For instance, colonizations under translucent rocks were mostly observed <25 mm thick and up to 40 mm thick, while lower abundances were observed under opaque rocks, generally of <15 mm and up to 30 mm thick (Berner and Evenari 1978). Other authors, e.g. Nienow and Friedmann (1993), found that hypolithic colonizations below quartz rocks ranged from several mm to 60 mm in depth. Microbial colonization beneath thicker rocks is confined to the periphery, as insufficient light to support photosynthesis is transmitted to the community at the base of the rock (Broady 1981b; Schlesinger et al. 2003).

9.4 Microbiology of Lithobionts

Lithobiontic diversity analysis was initially based on microscopic observations of morphological and ultrastructural features of cultured isolates (Friedmann 1980; Friedmann et al. 1988). More recently, culture-independent approaches have allowed a more comprehensive and representative knowledge of the composition of lithobiontic microbial communities (Khan et al. 2011; Smith et al. 2006; Pointing et al. 2009; Chan et al. 2013; Babalola et al. 2009; Makhalanyane et al. 2013a).

9.4.1 Epilith Diversity

Very little is currently known about epilithic microbiology, compared to the endolithic and hypolithic niches. By using culture-dependent approaches we know that *Chroococcidiopsis*, *Myxosarcina*, *Gloeothece*, *Plectonema*, *Lyngbya* and *Calothrix* species are commonly found in epilithic communities in Princess Elizabeth Land and Mawson Rock (Broady 1981a, b). In the same geographical area, 13 epilithic cyanobacterial species were identified (Broady 1989). Epiliths appear to be dominated by cyanobacterial taxa, perhaps as a consequence of their abilities to withstand UV irradiation (Campbell et al. 1998; Castenholz and Garcia-Pichel 2002). Further work, employing modern metagenomic approaches, is required to understand the “true” diversity of epilithic communities.

9.4.2 Endolith Diversity

Free cyanobacteria, together with lichenized structure, have been found to dominate endolithic communities (Friedmann et al. 1988). The cyanobacterium *Choroglea* sp. was detected in translucent gypsum crusts formed on sandstone surfaces on Alexander Island (Hughes and Lawley 2003). In the Taylor Valley, different genera of cyanobacteria, mainly *Chrocooccidiopsis* sp. with some *Cyanothece* cf. a*eruginosa* and *Nostoc* sp. (Büdel et al. 2008), have been identified. Cyanobacteria of the genera *Gloeocapsa* were first described in Victoria Land (Friedmann et al. 1988). Later, Friedmann et al. (1988) distinguished and characterized the diversity of the two types of cryptoendolithic communities inhabiting the Ross Desert: lichen-dominated and cyanobacterial communities. A total of 17 cyanobacteria from the McMurdo Dry Valleys were described. Depending on the dominant cyanobacterium, three communities were observed: *Gloeocapsa*, *Hormathonema–Gloeocapsa* and *Chroococcidiopsis*.

Using molecular techniques, lichenized endolithic communities were shown to be dominated by a single green algal species *Trebouxia jamesii* (de la Torre et al.

2003). *T. jamesii* is a known constituent of lichen associations, such as the lichenized fungal genus *Letharia* (Friedl and Rokitta 1997).

The analysis of the prokaryotic members of the community showed a diverse range of phylotypes related to Actinobacteria, α- and γ-Proteobacteria and Planctomycete species, and an abundance of uncultured bacteria (de la Torre et al. 2003). Clone libraries from endolithic communities showed a high actinobacterial diversity. Endoliths were dominated by cyanobacteria of the *Chroococcidiopsis* lineage (Friedmann 1982) and cyanobacteria morphologically similar to *Gloeocapsa, Plectonema* and *Hormathonema* species (Pointing et al. 2009; Wong et al. 2010b; de la Torre et al. 2003; de los Rios et al. 2004, 2005b).

9.4.3 Hypolith Diversity

The community structure and prokaryote species diversity of hypoliths are the best understood of all the lithobionts (Bahl et al. 2011; Chan et al. 2012, 2013; Cowan et al. 2010b; Khan et al. 2011; Makhalanyane et al. 2013b; Pointing et al. 2009). The prokaryotic composition of Antarctic hypolithons has been assessed using a range of approaches.

A combination of microscopy and culture-independent approaches has identified cyanobacteria as the predominant phylum in hypolithic colonization globally (Bahl et al. 2011; Lacap et al. 2010; Pointing et al. 2007; Stomeo et al. 2013; Warren-Rhodes et al. 2007), including Antarctica's McMurdo Dry Valleys and other ice-free areas (Broady 1981b, 2005; Smith et al. 2000; Pointing et al. 2009). Morphological studies suggest that cyanobacteria found in Antarctica and other cold deserts are dominated by filamentous oscillatorian morphotypes, with a lower species richness than other deserts (Smith et al. 2000; Chan et al. 2012). Communities in the Vestfold Hills showed the presence of oscillatorian cyanobacteria with morphologies typical of the *Lyngbya/Phormidium/Plectonema* group and coccoid cells morphologically similar to *Chroococcidiopsis* (Smith et al. 2000). Hypolithic communities have also been shown to harbour other bacterial phyla such as Actinobacteria, α- and β-Proteobacteria, Planctomycetes, Firmicutes, Acidobacteria and Verrumicrobia (Makhalanyane et al. 2013a; Bahl et al. 2011; Caruso et al. 2011). Archaeal phylotypes recovered were phylogenetically affiliated with a large group of uncultured *Crenarcheota* (Khan et al. 2011).

Although the majority of studies have focused on the bacterial composition in these communities (Bahl et al. 2011; Caruso et al. 2011; Makhalanyane et al. 2013a; Wood et al. 2008), there is evidence that the eukaryotic composition is more complex than initially anticipated (Khan et al. 2011; Gokul et al. 2013; Pointing et al. 2009). Eukaryotic phylotypic analysis showed that free-living ascomycetous fungi, chlorophytes and mosses were present in hypolithons (Khan et al. 2011). A detailed study focusing on the microeukaryotes in all three Antarctic hypolith types reported populations of novel uncharacterized Bryophyta, fungi and protists (Gokul et al. 2013). The presence of these taxa suggests that hypoliths may harbour quite complex food webs and therefore may be important in the cycling of nutrients in the cold desert oligotrophic environment.

Interestingly, it has been suggested that the different Antarctic hypolithic community morphotypes represent sequential stages of succession (Makhalanyane et al. 2013b; Cowan et al. 2010b). The bacterial community compositions of the three hypolith types in the east Antarctic Miers Valley show separate and statistically significant clustering. Using a probabilistic dissimilarity matrix analysis (Makhalanyane et al. 2013b), the species composition (beta-diversity) was shown to vary between different sites and was found to be higher in Type I hypolithons than in Types II and III. These differences suggest that deterministic processes in the bacterial component of hypolithons might increase in the order Type I => Type II => Type III. As it is currently assumed that the effects of stochastic variation may become less important as communities develop over time (Fierer et al. 2010), these findings suggest that the Type I (cyanobacteria-dominated) hypolithic community might be the founder community in the succession process. These patterns have important implications as communities of higher beta-diversity are likely to be vulnerable to climate change (McKnight et al. 2007).

9.5 The Role of Lithobionts in Depauperate Environs

Lithobionts are widely dispersed in depauperate environments (Broady 1981b, 2005; Pointing and Belnap 2012; Chan et al. 2012), and in Antarctic terrestrial ice-free environments lithobiontic are often the only primary producers. Hypoliths, which are by far the most widely distributed Antarctic lithobionts, were shown to cover up to 66 $cm^2\ m^{-2}$ in some regions and contributed up to 0.85 mg chlorophyll m^{-2} of total biomass (Broady 1981b). Moreover, in the Arctic, the productivity of hypolithons was estimated to be approximately $0.8 \pm 0.3\ g\ m^{-2}$. Given the fact that the total average productivity from plants, lichens and bryophytes in the same area was only $1.0 \pm 0.4\ g\ m^{-2}$ (Bliss et al. 1984), hypolithic productivity was estimated to almost double the productivity estimates (Cockell and Stokes 2004). All together these results suggest hypolithic communities potentially represent a major fraction of the total photosynthetic capacity in Antarctic terrestrial ecosystems.

Hypoliths have also been shown to possess the both the genetic and functional capacity for nitrogen fixation (Cowan et al. 2011b). Nitrogenase activity, determined using the acetylene reduction assay, estimated that total contribution of hypolithic communities to the Miers Valley region at approximately 14,200 mmol N $year^{-1}$ (0.38 kg N $year^{-1}$), indicating that these communities are important contributors to fixed nitrogen budgets in Antarctic Desert soils. In consequence, the direct contribution of lithic communities to the total carbon and nitrogen turnover in cold desert ecosystems may be highly significant (Cowan et al. 2011b; Hopkins et al. 2009; Chan et al. 2012).

A recent investigation to establish metabolic capabilities in lithobionts (chasmoendoliths, cryptoendoliths and hypoliths) and open soil from the

McKelvey Valley, using a metagenomic approach with GeoChip-based functional gene arrays, was able to reveal certain functional traits that drive community assembly and microbial survival (Chan et al. 2013). This study identified, for the first time, the primary metabolic pathways in lithobionts and showed a high level of genetic plasticity in autotrophs, heterotrophs and diazotrophs. Important differences were found between the open soil, hypolithic and endolithic communities, with new pathways reported for stress-, thermal-, osmotic-responses and nutrient limitation in lithobionts (Chan et al. 2013). The results of this study add substantially to our knowledge of the critical roles played by lithobionts in the Antarctic Desert ecosystem.

9.6 Concluding Remarks

The apparent simplicity of lithobiontic communities makes them good model systems for studies assessing community origins and evolution, trophic functioning and interspecies relationships, and for addressing wider ecological questions. For example, understanding the assembly patterns in hypoliths could shed light on how microbial guilds in other environments might respond to different stressors. Lithobionts may also be good markers for aridity and climate change and may also serve as “ecosystem engineers” (Chan et al. 2012).

Since the initial explorations of the Antarctic lithobiontic ecological niche, we understand considerably more about the microbial diversity within these communities. We are, however, only beginning to learn about their community function and community dynamics, i.e. beta-diversity patterns and the factors that drive them. Modern “omics-based” approaches are potentially very valuable in revealing both the functional capacities and adaptive potentials of microbial communities. For instance, the coordinated use of proteomic and transcriptomic methods could give insight into key metabolic functions and their responses to macro- and microenvironmental changes. There are, however, severe methodological limitations, not the least that both biomass levels and intrinsic process rates are typically low in in situ Antarctic Desert communities. Such limitations notwithstanding, an understanding of the functional guilds in Antarctic lithobiont communities has a particular significance, as these communities are likely to be the basis for the survival of the entire ecosystem.

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Chapter 10
Microbial Ecology of Geothermal Habitats in Antarctica

Craig W. Herbold, Ian R. McDonald and S. Craig Cary

Abstract Geothermal features in Antarctica generate liquid water and establish physicochemical gradients that provide habitat for diverse microbes. Studies on the microbial ecology of these features using traditional techniques have shown that the high-altitude, continental volcanoes (Mt. Erebus, Mt. Melbourne and Mt. Rittmann) possess microbial communities that share key taxa and are unique from the communities found in the distant geothermal habitats at Deception Island. In recent years, the application of molecular work has revealed the presence of potentially endemic organisms that previously escaped detection. While still in its infancy, the application of molecular strategies promises to revolutionize our current understanding of this habitat.

10.1 Introduction

Geothermal habitats in Antarctica are small oases of heat and liquid water in an otherwise vast, dry, and cold environment. Four volcanoes south of the 60°S parallel host small areas of geothermal habitat, three are in the continental setting of Victoria Land, and one is in the maritime setting of the South Shetland Islands. Physicochemical gradients generate a range of surface and subsurface environments that are suitable for a diversity of microbial life adapted to "neutral"

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conditions as well as extremes of temperature and pH (Broady 1984; Broady et al. 1987; Bargagli and Broady 1996; Soo et al. 2009). Locally heterogeneous populations are supported by these physicochemical gradients, and in some cases localized geochemistry contributes to this heterogeneity (Bargagli et al. 1993). The island-like nature and localized heterogeneity make Antarctic geothermal locations ideal for studying biogeography and evolution. It has even been suggested that these areas may also be surface manifestations of the "deep biosphere" (Gold 1992), allowing access to ancient and unique microbial lineages (Soo et al. 2009).

Studies on the microbial ecology of these areas have primarily emphasized "macroflora" assemblages of bryophytes, algae, and cyanobacteria as well as heterotrophic bacilli. These assemblages have been studied using a combination of microscopy and cultivation techniques which have shown that the communities at high-altitude, continental volcanoes (Mt. Erebus, Mt. Melbourne, and Mt. Rittmann) possess microbial communities that are low in diversity and taxonomically unique from the communities found in the distant geothermal habitats at Deception Island. It is still unclear whether differences in community composition between volcanoes, and between sites on the same volcano, are driven more by biogeography, or physicochemical controls.

In this chapter, we first introduce the volcanoes of Antarctica and then focus on the four volcanoes known to host geothermal habitats. We then describe each of these habitats in detail to orient the reader to the features of each location and discuss the individual organisms that have revealed important information about these habitats, and their distributions. We then introduce the various organisms that have been cultivated and/or observed and what each has contributed to our understanding of microbial ecology of geothermal habitats in Antarctica. We included a discussion on mosses and liverworts because mosses do not develop past the protonemal stage at Mt. Erebus (Broady 1984) and thus for all intents and purposes, they are members of the microbial community. Finally, we discuss the current and anticipated advances that molecular tools are providing.

10.2 Antarctic Volcanoes and Associated Geothermal Habitats

Geothermal habitats in Antarctica typically consist of heated mineral soils found near fumarolic steam vents and/or fissures and are exclusively associated with geologically active volcanoes. The Global Volcanism Program (http://www.volcano.si.edu) lists many potentially active volcanoes in and around Antarctica that have erupted within the Pleistocene (2.6 Mya to 11.7 kya) or Holocene (11.7 kya to present) (Fig. 10.1). Six of these are located in Victoria Land (East Antarctica) and six are located in Marie-Byrd Land (Western Antarctica). Additional volcanic islands are also associated with Antarctica: Mt. Erebus (Ross Island), Siple Island, Peter I Island, three volcanoes within the Balleny islands, three volcanoes

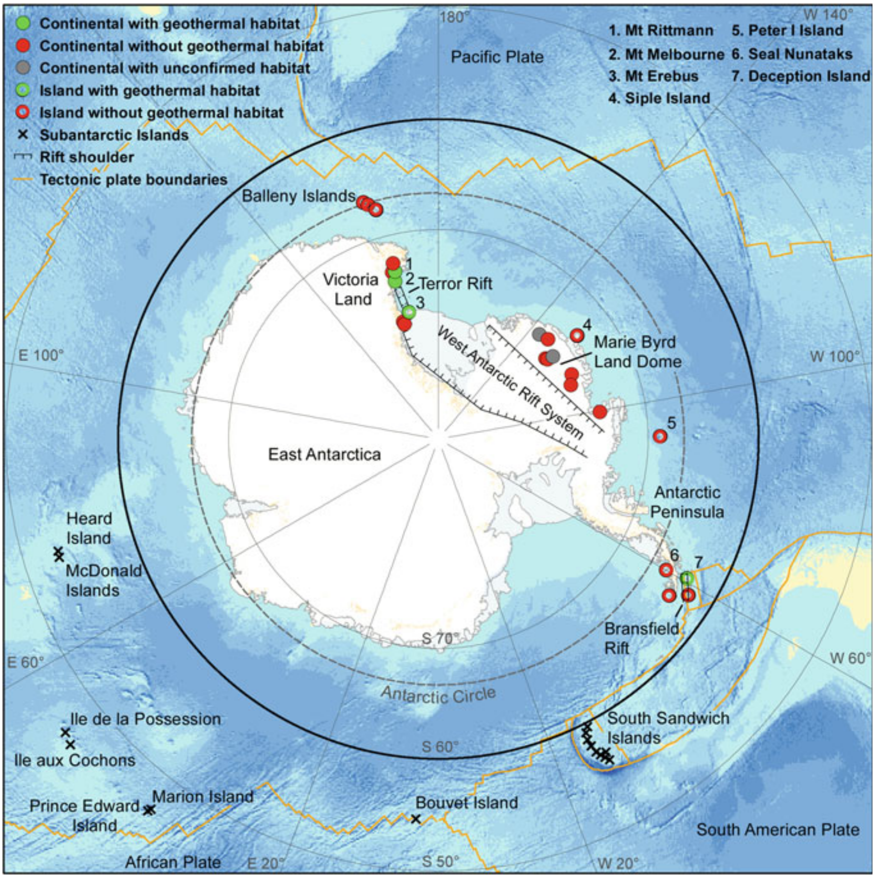


Fig. 10.1 Locations of Volcanoes and major tectonic features in and near Antarctica (illustration by Glen Stichbury)

within the South Shetland Islands, and sixteen small islands that comprise the Seal Nunataks. There are also numerous volcanic islands in "subantarctic" areas, including volcanoes within the Sandwich Islands, and in the Southern Atlantic and Indian Oceans. These "subantarctic" volcanic islands (north of 60°S latitude) are often discussed in comparisons to Antarctic continental geothermal habitats, however, are beyond the scope of this chapter.

Most currently active Antarctic volcanoes arise from processes and features associated with rifting zones, in particular the West Antarctic rift system (WARS). The WARS extends approximately 3,000 km (Fig. 10.1), encompassing the Ross Sea and extending across Antarctica to the base of the Antarctic Peninsula (Behrendt et al. 1991). Marie-Byrd Land dome is located on the northern edge of the WARS and active volcanism there is probably linked to a localized hot spot system (Winberry and Anandakrishnan 2004). Victoria Land is located along the western Ross Sea, on the southern edge of the WARS and active volcanism there is constrained to the Erebus and Melbourne volcanic provinces (Kyle and Cole 1974). Specifically, Mt. Erebus and Mt. Melbourne are situated at either end of the Terror rifting zone, a smaller rifting zone within the larger WARS (Kyle 1990). Deception Island is located within the South Shetland Islands and is associated with the Bransfield rift spreading center, a rifting zone that is not associated with the WARS but is instead a marginal basin arising from complex tectonic interactions between the Antarctic, Pacific, Scotia, and (former) Phoenix Plates (Barker and Austin 1998).

Several volcanic islands near Antarctica probably arise from island-forming processes that are poorly understood and may be unrelated to rifting zones. The Balleny islands for instance are a volcanic island arc located along a complex submarine ridge system that extends from Antarctica to New Zealand (Verwoerd et al. 1990) but has probably arisen from a volcanic hot spot that may also be responsible for several seamounts in the Tasman Sea (Lanyon et al. 1993). Siple Island is a shield volcano off the coast of West Antarctica (LeMasurier 1990), and Peter I island is a shield-like seamount (Verwoerd et al. 1990). The seal nunataks are either several small stratocones or shield volcanoes (Smellie 1990); however, it is currently unclear what tectonic processes are responsible for their formation.

Most of the volcanoes in Antarctica do not currently show any signs of volcanic activity, and only four are known to contain geothermal habitats. Three are located in Victoria Land (Mt. Erebus, Mt. Melbourne and Mt. Rittmann), and the fourth is Deception Island in the South Shetland Island group (Fig. 10.1). Three additional volcanoes in Antarctica are suspected geothermal habitats: Mt. Hampton, Mt. Kauffman, and Mt. Berlin. Actively steaming ice chimneys have been observed at Mt. Berlin and Mt. Kauffman (LeMasurier and Rex 1982), suggestive of active venting. Mt. Hampton also possesses fumarolic ice chimneys such as those found on Mt. Berlin and Mt. Kauffman, but these were not actively steaming when last observed (LeMasurier and Wade 1968; Wilch 1997). The presence of these features suggests ongoing geothermal activity, and hence geothermal habitat potential, since erosive processes would be expected to wear ice chimneys away over short timescales (LeMasurier and Wade 1968). Regardless, these volcanoes are largely inaccessible, and at this time, no samples have been collected for biological investigation. Therefore, it is not known whether these features support geothermal ecosystems, and if they do what types of organisms are present.

The three volcanoes that have contributed most significantly to our understanding of geothermal ecosystems in Antarctica (Deception Island, Mt. Erebus, and Mt. Melbourne) are “easily” accessible due to the proximity of scientific research stations and have historical significance, having been discovered and described in the early nineteenth century. The sunken caldera of Deception Island forms Port Foster, which has provided a safe haven for ships since its discovery in 1820; meanwhile, both Mt. Erebus and Mt. Melbourne were discovered by Captain James Clark Ross in 1841. The relative accessibility of these volcanoes has also contributed toward their sustained role in scientific study. Prior to the devastating eruptions of 1967–1970, Deception Island hosted three scientific research stations run by the UK, Chile, and Argentina. Mt. Erebus is located on the same island (Ross Island) as McMurdo Base (USA) and Scott Base (NZ). The summit of Mt. Melbourne is approximately 50 km north of Mario Zuchelli Station (ITA), Gondwana Station (GER), and the site of the new Jang Bogo Station (Korea). The important role that these volcanoes play in scientific research has been readily acknowledged, and each hosts at least one Antarctic Specially Protected Area (ASPA), that is protected by an international treaty. Mt. Rittmann, on the other hand, is the least studied volcano with a known geothermal habitat and also happens to be the furthest away from a base (approx. 100 km north of Mt. Melbourne and 150 km north of Italy's Mario Zucchelli Base), and the only one of the four for which there is currently no protection.

10.2.1 High-Elevation Geothermal Habitats of Victoria Land

Geothermal habitats in Victoria Land can be found on three volcanoes located in the McMurdo Volcanic Group, a massive field of mostly extinct volcanoes that have been divided into volcanic "provinces" based on geography and geochemistry (Kyle and Cole 1974). In the Erebus volcanic province, active geothermal habitats are restricted to Mt. Erebus (Ugolini and Starkey 1966), and geothermal habitats in the Melbourne volcanic province are restricted to Mt. Melbourne (Nathan and Schulte 1967) and Mt. Rittmann (Bargagli and Broady 1996). These three volcanoes possess high-altitude, geothermal habitats that are all chemically similar to one another (Bargagli and Broady 1996) and support similar assemblages of cyanobacteria, green algae, and moss (Broady 1984; Broady et al. 1987; Bargagli and Broady 1996; Bargagli et al. 2004).

10.2.1.1 Mt. Erebus

Mt. Erebus (167.17°E 77.53°S; 3,794 m) is a stratovolcano located on Ross Island in the western Ross Sea. It is the southernmost active volcano on Earth, has a persistent convecting phonolitic lava lake, and experiences daily strombolian eruptions (Kyle 1990). The volcanic activity of Mt. Erebus is associated with crustal thinning in the western Ross Sea as a result of rifting processes (Kyle 1990), and possibly a mantle plume or hot spot (Kyle and Muncy 1989). Mt. Erebus originated as a subaerial volcano, transitioning from shield-building to proto-cone-building approximately one million years ago (Esser et al. 2004). The modern cone-building phase of Erebus began approximately 240,000 years ago and the summit plateau was most likely formed by summit collapse from a draining magma chamber approximately 90,000 years ago (Esser et al. 2004). It is likely that the summit caldera of Erebus has evolved through subsequent magma chamber collapse, low-volume lava flows and small explosive events over the last

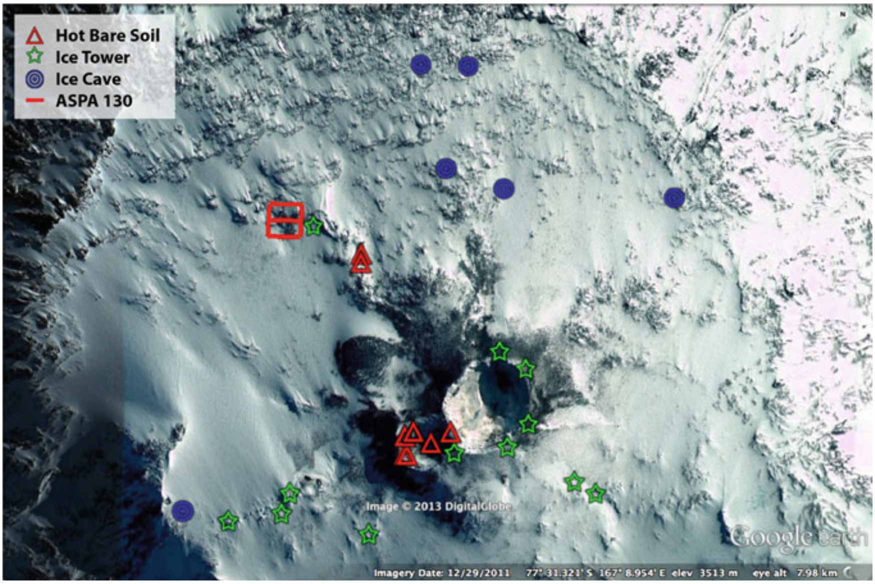


Fig. 10.2 Representative geothermal features on the summit caldera of Mt. Erebus. Hot bare soils are marked with *red triangles*, ice chimneys/towers are marked with *green stars,* and ice caves are marked with *blue circles*. Boundaries of ASPA 130 are marked with *red lines*

90,000 years with at least one major Plinian eruption (sending ash and gas high into the upper atmosphere) approximately 40,000 years ago (Harpel et al. 2004).

Persistent geothermal activity on the summit plateau of Mt. Erebus heats ice and the processes of evaporation and condensation create dynamic ice caves, ice chimneys, and towers (Fig. 10.2). These ice features are being actively monitored each summer by members of the Mount Erebus Volcano Observatory (MEVO) based at the New Mexico Institute of Mining and Technology, who maintain an informative database of all currently known ice caves and ice towers on Mt. Erebus (http://erebuscaves.nmt.edu/) and are studying these features to understand how they form and change over time. Erebus Ice towers and chimneys are thought to be formed over extensive ice cave systems at locations where heat flux is low; however, where heat flux is greater, bare, steaming mineral soils persist with fumaroles that emit steam and CO_2, providing a near constant year-round source of moisture and heat (Broady 1984; Hudson and Daniel 1988; Soo et al. 2009). On Mt. Erebus, bare soils are found near the summit of the main crater, within the adjacent side crater, and in an extensive terraced area known as Tramway Ridge (ASPA 130). The Tramway Ridge ASPA is located approximately 1.5 km NW of the main crater and has been the topic of several descriptive and recent microbiological investigations (Ugolini and Starkey 1966; Ugolini 1967; Hudson and Daniel 1988; Hudson et al. 1989; Broady 1984; Soo et al. 2009; Nicolaus et al. 2001).

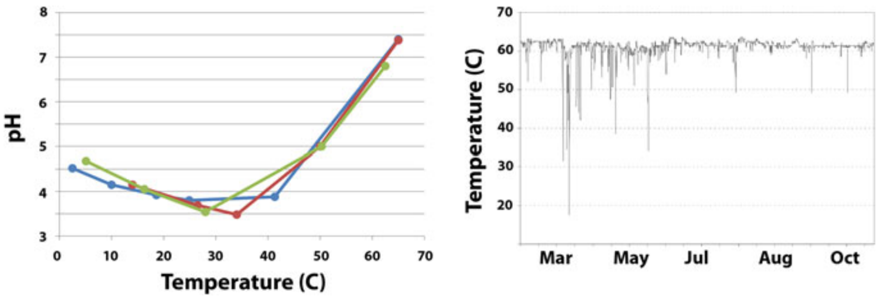


Fig. 10.3 *Left* relationship between temperature and pH in 3 transects of mineral soils adjacent to fumaroles at Tramway Ridge. *Right* temperatures recorded adjacent to a fumarole over a ten-month period in 2006 (Soo et al. 2009)

The Tramway Ridge ASPA is located on a gentle southern-facing terraced slope at the terminus of a lava flow that is approximately 9,000 years old (Broady 1984; Harpel et al. 2004) and is split into two areas, each approximately 100 m × 50 m. The southern, lower half is accessible to scientists through a permitting process, while the northern half is a prohibited area (ASPA 130 management plan). Steam fumaroles provide a warm, moist microclimate (Ugolini 1967) where surface temperature can reach 65 °C and pH is neutral to mildly alkaline (Hudson and Daniel 1988; Soo et al. 2009). Soils adjacent to fumaroles exhibit sharp temperature and pH gradients, with surface temperatures reaching 0 °C within 0.5 m of fumaroles, and pH recordings as low as 3.5 within 10 cm of fumaroles (Soo et al. 2009). A clear relationship can be seen between temperature and pH; the highest pH corresponds with the highest temperatures (Fig. 10.3), and the lowest pH is found between 25 and 40 °C. Temperature loggers deployed over winter in Tramway Ridge fumeroles show that temperature is relatively constant, even during winter; however, sharp downward spikes sometimes lasting over 24 h are common occurrences (Fig. 10.3) (Soo et al. 2009).

Tramway Ridge has conspicuous zonation patterns driven by its steep temperature and pH gradients. In Broady's (1984) study, 5 types of biological mat zones were defined: (1) bare ground; (2) green crusts found in small crevices and depressions and superficially covered by sediment; (3) green surface crusts; (4) red-brown felt at surface; (5) dark gray to almost black felt. The conspicuous visual differences between different "types" of mats were directly tied to the temperature zonation and the taxonomic composition of microscopically identifiable moss, algae, and cyanobacteria in the different mats (Broady 1984). Likewise, Soo et al. (2009) found that differences in pH, temperature, and moisture content best correlate to differences in bacterial communities inhabiting the subsurface at Tramway Ridge.

10.2.1.2 Mt. Melbourne

Mt. Melbourne (164.42°E 74.21°S; 2,732 m) is a stratovolcano located on a peninsula bordering Campbell Glacier, and Wood and Terra Nova Bays in northern Victoria Land (Kyle 1990). Mt. Melbourne is part of a local volcanic field of subglacial and subaerial volcanoes that encompasses most of the peninsula and extends into the adjacent bays (Wörner and Viereck 1987). Like Mt. Erebus, its volcanic activity is associated with crustal thinning in the western Ross Sea as a result of rifting processes (Kyle 1990), and there is some evidence that it has erupted sometime in the last 200 years (Lyon 1986).

Numerous geothermal features are located on or near the summit of Mt. Melbourne, following a general NW–SE line, which includes short ice hummocks, ice towers up to 7 m high, bare patches of heated ground and "cold" ground that nevertheless shows signs of hydrothermal alteration (Nathan and Schulte 1967; Lyon and Giggenbach 1974). The biological communities at five sites of bare, heated ground have been studied (Broady et al. 1987) and found to host a diverse assemblage of bryophytes and algae that was unique enough to warrant special protection of the entire summit above 2,200 m as ASPA 118. Similar to Tramway Ridge on Mt. Erebus, this ASPA is divided into 2 "managed zones" (restricted and prohibited) in order to assure protection of the unique biodiversity (ASPA 118 Management Plan). The managed zones encompass markers used in deformation studies, while the restricted and prohibited zones refer exclusively to "Cryptogram Ridge" (site A in Fig. 10.4). The remaining sites that are known to host biological communities (B–D in Fig. 10.4) have no specific protection besides being part of the ASPA located above the 2,200 m contour. Biological studies at Mt. Melbourne have focused on two sites, "Cryptogram Ridge" (site A in Fig. 10.4) and the "Northwest Slope" (NW slope) (site E in Fig. 10.4) (Broady et al. 1987; Bargagli et al. 2004).

Cryptogram Ridge is located within the caldera of Mt. Melbourne, curving around the north and northeast edges of an old crater rim and encompasses an area of approximately 100 m × 20 m. Steam vents are found where the ground is hottest (42 °C), and the mineral soils tend to be fine-grained and altered compared to cooler areas (Broady et al. 1987). Low-lying ice hummocks are found where the spacing between steam vents is larger and the ground is generally cooler (Broady et al. 1987). Temperature profiles taken along transects at Cryptogram Ridge suggest that a relatively large volume of the subsurface is heated to approximately 60 °C, and that geothermal flux away from this deeper heat reservoir is concentrated at the hottest ground by convection (Broady et al. 1987). The pH of the mineral soil at Cryptogram Ridge is only known from a single measurement of a bulked soil sample (pH 5.1); therefore, it is unclear whether mineral soils in this site exhibit the same relationship of temperature and pH apparent at Tramway Ridge, Mt. Erebus.

The largest ice towers (7 m) and hottest surface measurements (49.5 °C) at Mt. Melbourne are found on its "NW Slope" where at least two patches of bare, hot

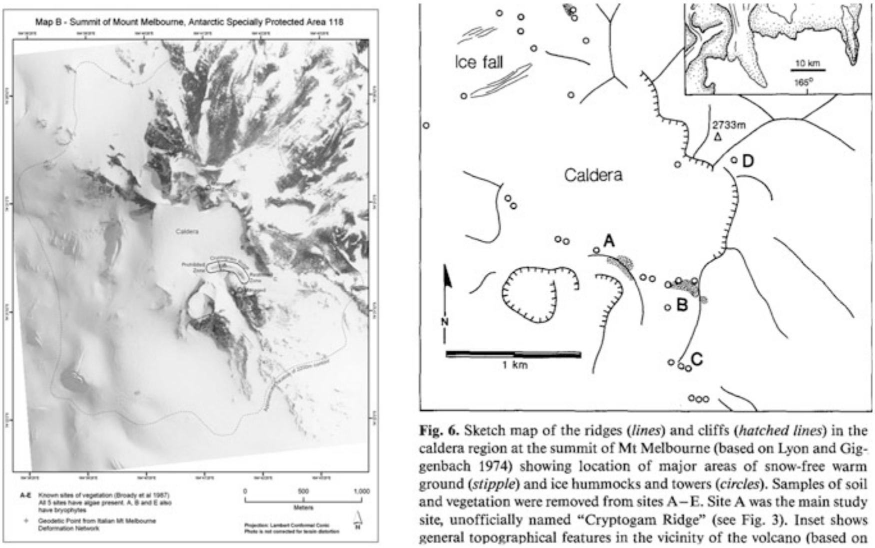


Fig. 6. Sketch map of the ridges (*lines*) and cliffs (*hatched lines*) in the caldera region at the summit of Mt Melbourne (based on Lyon and Giggenbach 1974) showing location of major areas of snow-free warm ground (*stipple*) and ice hummocks and towers (*circles*). Samples of soil and vegetation were removed from sites A – E. Site A was the main study site, unofficially named "Cryptogam Ridge" (see Fig. 3). Inset shows general topographical features in the vicinity of the volcano (based on

Fig. 10.4 Summit of Mt. Melbourne. *A–E* are sites of geothermal habitats. *Left* Map B from ASPA 118 management plan. *Right*, Fig. 10.6 from Broady (1987). Site *A* is known as "Cryptogram Ridge" and site *E* is the "Northwest Slope"

ground containing fumaroles have been reported (Nathan and Schulte 1967; Lyon and Giggenbach 1974; Broady et al. 1987). Several studies suggest that the biological communities there differ from those found at Cryptogram Ridge and that this difference may be related to different geochemistry, in particular iron bioavailability, between the two sites (Bargagli et al. 2004; Pepi et al. 2005).

10.2.1.3 Mt. Rittmann

Mt. Rittmann (165.50°E 73.45°S, 2,600 m) is located about 110 km N of Mt. Melbourne and is bordered by the Aviator, Pilot, and Icebreaker Glaciers. It was discovered much more recently than the other volcanoes in Victoria Land (Armienti and Tripodo 1991), and extensive fumarolic activity is taken as a sign that it is still active (Bonaccorso et al. 1991). Like Mt. Erebus and Mt. Melbourne, its volcanic activity is probably associated with crustal thinning in the western Ross Sea as a result of rifting processes (Kyle 1990; Antonini et al. 1994); however, there is considerably less known about this volcano than either Mt. Melbourne or Mt. Erebus.

Geothermal habitats at Mt. Rittmann are restricted to fumarolic mineral soils located on a single, steep face, approximately 200 m wide and 80 m high near the caldera rim (Fig. 10.5) (Bargagli and Broady 1996). Surface temperatures can be as high as 43.4 °C and temperature at a depth of 10 cm can reach 63 °C (Bargagli

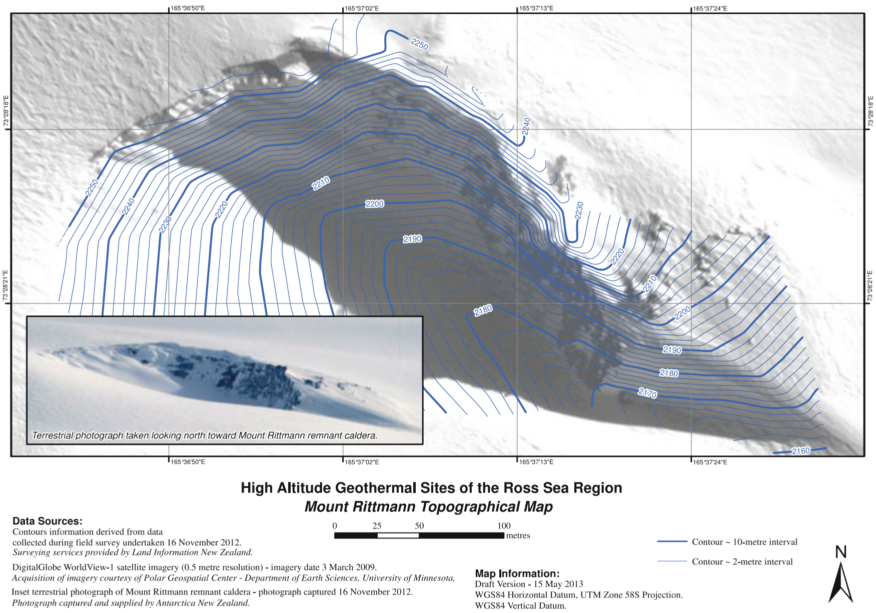


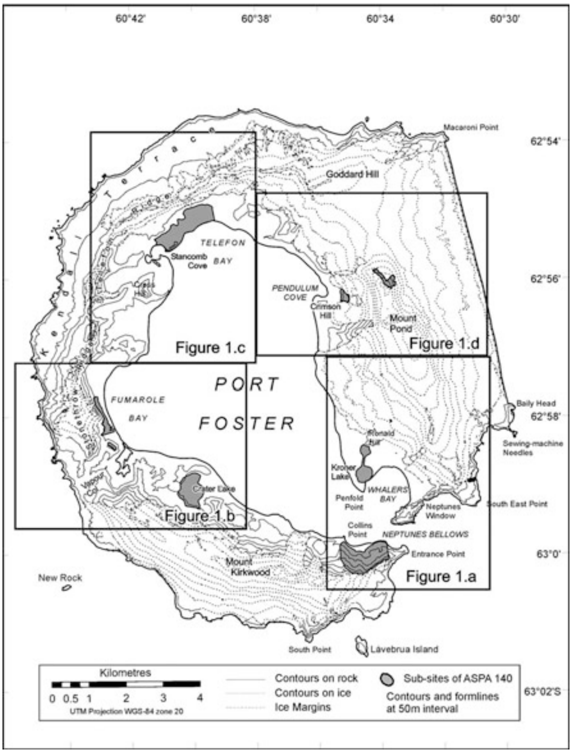
Fig. 10.5 Mt. Rittmann topographical map. Geothermal areas are ice-free. (illustration by Trent Gulliver)

and Broady 1996). Overall pH of the site is reported as 5.4 ± 0.2, but as is the case for Mt. Melbourne, there has been no attempt to correlate pH and temperature measurements of individual samples. Soils are described as a fine gravelly medium sand, in which the grain-size and surface area of grains do not favor the adsorption of organic matter or water extractable nutrients (Bargagli and Broady 1996). Mt. Rittmann is currently not protected; however, there are current efforts led by Antarctica New Zealand to establish an ASPA modeled after the ASPAs for Tramway Ridge, Mt. Erebus, and Mt. Melbourne summit.

10.2.2 *Low-Elevation Geothermal Habitat of Deception Island*

Deception Island (60.67°W 63.00°S; 0–542 m) is the caldera rim of a submerged polygenetic shield volcano that last erupted between 1967 and 1970 (Smellie 1990). It is located at the southwest end of the South Shetland Islands, near the tip of the Antarctic Peninsula. It is one of at least five volcanic centers located along the Bransfield Rift spreading center (Barker and Austin 1998), and the only one whose summit is higher than sea level. All visible parts of the island are dated to sometime within the last 700,000 years (Valencio et al. 1979). The oldest rocks are

Fig. 10.6 Subsites that are specifically protected in ASPA 140 management plan are labeled *A–L*



located on the external slopes of the caldera, while continuing volcanic activity has acted to remodel the internal features of the crater (Smellie 1990). Continuing activity at Deception Island has been well documented in historical times. A period of activity lasting from 1967 to 1970 reshaped the inner crater geography, and in the process completely destroyed the Chilean base at Pendulum Cove and badly damaged the British base at Whalers Bay.

The submerged Caldera of Deception Island is known as Port Foster. Ships can sail into Port Foster through an opening known as Neptune's Bellows at the Southeast of the island. Strangely enough, this violently volcanic port provided a safe haven from extreme weather for whaling ships and Deception Island became a hub for whaling activity in the Southern Ocean in the nineteenth century. Thus, unlike the high-altitude continental volcanoes of Victoria Land, Deception Island is no stranger to visitors, hosts a penguin colony, and is a common destination for Cruise ships with tourists who enjoy bathing in the warm hot water at Pendulum Cove each summer.

The recognition that Deception Island is "mixed-use" is apparent in the regulations set forth in the management plan (ASPA 140), and while the entire island is "managed," specific protections have been reserved for locations that have identified, unique assemblages of vegetation. This has resulted in the protection of 11 subsites around Deception Island (Fig. 10.6), 7–8 of which contain geothermal habitats. Several of these are submarine or partially submarine, and host unique algal communities (Fermani et al. 2007). Nearly all sites of geothermal activity are thought to originate from the volcanic activity of 1967–1970, and thus are relatively young. The only exception is the area at Mount Pond (subsite H), which is thought to be much older and is considered the most important botanical site on the island (Lewis-Smith 2005). Given the continuing activity at Deception Island thermal areas, definitions are a somewhat moving target. The eruption in 1967 created a new island of cinder cones in Telefon Bay (Valenzuela et al. 1968; Baker et al. 1969) that provided a newly formed soil site to study processes of colonization (Cameron and Benoit 1970). However, subsequent eruptions completely destroyed this site, creating new ones in the process (Smith 1974).

10.3 Life in Antarctic Geothermal Habitats

In Antarctic geothermal areas, visual evidence of living organisms can range from a greenish tinge of soil surrounding fumaroles to the presence of lush moss hummocks. The conspicuousness of the “flora” component of these communities has drawn attention from botanists and algologists, and subsequently the protection of these sites has been largely driven by an interest in phototrophic communities (ASPA guidelines for 118, 130, 140, Lewis-Smith 2005). Yet, the catalog of organisms found associated with geothermal habitats in Antarctica includes far more than the conspicuous phototrophic communities. The presence of a point source of heat, in an otherwise freezing environment, provides a range of microhabitats, supporting the growth of thermophiles in the hottest locations, but also of mesophiles in the cooler margins, all exhibiting a zonation clearly reflecting their competitive growth temperatures (Broady 1984). Phototrophic prokaryotes, followed by algae, and finally moss, are found as one progressively moves from hotter to cooler areas. Protozoans appear to be restricted to cooler areas and are associated with moss, while spore-forming fungi and bacteria have been isolated from a wide range of temperature environments.

10.3.1 Eukaryotes

Moss and algae dominate the eukaryotic component of communities found in geothermal habitats, while heterotrophic Eukaryotes, such as protozoa and fungi, are found in much lower numbers. Eukaryotes have been found in each of the four well-studied geothermal locations in Antarctica (Janetschek 1963; Broady 1984; Broady et al. 1987; Ugolini and Starkey 1966; Bargagli and Broady 1996; Cameron and Benoit 1970), where they are restricted to zones below 40 °C (Broady 1984). The diversity of bryophytes, algae, and protozoa is noticeably higher at the geothermal locations of Deception Island compared to the three high-altitude sites

(Mts. Erebus, Melbourne, and Rittmann). This dichotomy is not as apparent in the literature covering prokaryotic communities; however, it should be cautioned that until very recently prokaryotic studies have been almost entirely focused on culturable taxa.

10.3.1.1 Bryophytes (Mosses and Liverworts)

The relative paucity of bryophyte species in the high-altitude geothermal habitats of continental Antarctica contrasts the highly diverse bryophyte communities associated with thermal areas at Deception Island, where there are at least 49 documented species of moss and 9 documented species of liverwort (Lewis-Smith 2005). It is currently unknown if this remarkable difference is due to the greater degree of isolation of the high-elevation sites, local geochemistry, or the difference in diel cycles associated with the more southern high-elevation sites experiencing constant light in summer and constant darkness in winter. In this section, we have purposefully omitted a thorough characterization of the bryophytes present on Deception Island, mentioning them only in cases where specific taxa co-occur in one of the three high-altitude geothermal areas. In terms of bryophyte communities, Deception Island appears to have more in common with the South Sandwich Islands and other sub-Antarctic islands with geothermal activity, and interested parties are encouraged to investigate recent reviews for more information on bryophytes of Deception Island (Lewis-Smith 2005) and/or the South Sandwich Islands (Convey and Lewis-Smith 2006).

Two species of moss (*Campylopus pyriformis* and *Pohlia nutans*), and one species of liverwort (*Cephaloziella exiliflora* syn. *C. varians*), have been observed in different areas of Mt. Melbourne. *C. exiliflora* and *C. pyriformis* are found only at Cryptogram Ridge, while *P. nutans* is found only on the NW Slope. The two mosses also have non-overlapping ranges beyond Mt. Melbourne: *C. pyriformis* is found at Tramway Ridge, Mt. Erebus, while *P. nutans* is found at Mt. Rittmann and on Deception Island (Table 10.1). All three bryophyte species are found in non-Antarctic locations in both the Southern and Northern Hemispheres.

Campylopus pyriformis is found in locations with surface temperatures of 20–30 °C, but also in cracked crusts covered by a small layer of sediment (<1.0 cm deep) down to temperatures of 10 °C. The strain of *C. pyriformis* that was collected from Tramway Ridge, Mt. Erebus, exists only as a velvety green surface crust of undifferentiated protonema and is incapable of maturing into gametophytes, even under cultivation (Broady 1984; Skotnicki et al. 2001). This trait justifies its inclusion as part of the "microbial" ecosystem at Tramway Ridge; however, the strain of this species from Cryptogram Ridge, Mt. Melbourne, lacks this trait and is capable of forming mature gametophytes under cultivation (Broady et al. 1987). Despite the obvious developmental differences between their populations, *C. pyriformis* at Mt. Erebus and Mt. Melbourne have been shown to be closely related genetically and may have arisen from a single colonization event at

Table 10.1 Geographical distribution of microbes identified from Antarctic geothermal features

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
Bacteria						
Firmicutes	*Alicyclobacillus acidocaldarius*	C	C			Hudson and Daniel (1988), Hudson et al. (1988, 1989), Gul-Guven et al. (2007, 2011), Wisotzkey et al. (1992), Faraone-Mennella et al. (2006)
	Alicyclobacillus pohliae			C^b		Bargagli et al. (2004), Pepi et al. (2005), Imperio et al. (2008)
	Aneurinibacillus terranovensis		C	C^a		Logan and Allan (2008), Allan (2005)
	Anoxybacillus amylolyticus		C			Poli et al. (2006, 2009)
	Bacillus fumarioli		C	C^a		Logan et al. (2000)
	Bacillus licheniformis				C^k	Llarch et al. (1997)
	Bacillus megaterium				C^k	Llarch et al. (1997)
	Bacillus schlegelii	C				Hudson and Daniel (1988), Hudson et al. (1988)
	Bacillus sp.	C		C^a	$C^{c,f,k}$	Hudson and Daniel (1988), Broady et al. (1987, Cameron and Benoit (1970), Llarch et al. (1997), Nicolaus et al. (1991)
	Brevibacillus levickii			C^b		Logan and Allan (2008, Allan (2005)
	Geobacillus jurassicus subsp Deception Island				C d	Muñoz et al. (2011)
	Geobacillus thermoantarcticus			C a		Nicolaus et al. (1991, 1995, 1996), Lama et al. (1996, 2001, 2004), Manca et al. (1996), Faraone-Mennella et al. (2006), Zeigler (2005), Dipasquale et al. (2008), Poli et al. (2009), Coorevits et al. (2012), Çalık et al. (2009)
	Clostridium sp.	C				Hudson and Daniel (1988)
Actinobacteria	*Arthrobacter* sp.			C^b		Bargagli et al. (2004)

(continued)

Table 10.1 (continued)

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
	Corynebacterium sp.				C^f	(Cameron and Benoit 1970)
	Micrococcus sp.	C		C^a	C^f	Broady et al. (1987), Cameron and Benoit (1970), Nicolaus et al. (1992, 2001)
	Mycobacterium sp.				C^f	Cameron and Benoit (1970)
	Nocardia sp.				C^f	Cameron and Benoit (1970)
	Streptomyces coelicolor	C		C^a		Broady et al. (1987)
	Thermomonospora sp.	C		C^a		Broady et al. (1987)
Cyanobacteria	*Aphanocapsa elachista*	OC		O*		Broady (1984), Broady et al. (1987)
	Gleitlerinema sp.				O^k	Izaguirre et al. (2006)
	Gloeocapsa magma			$O^{a,b}$		Broady et al. (1987)
	Leptolyngbya foveolarum				O^k	Izaguirre et al. (2006)
	Leptolyngbya fragilis				O^k	Izaguirre et al. (2006)
	Leptolyngbya frigida				C^c	Fermani et al. (2007)
	Leptolyngbya glacialis				C^c	Fermani et al. (2007)
	Leptolyngbya sp.				O^d	
	Lyngbya sp.		C			Bargagli and Broady (1996)
	Mastigocladus laminosus	OC	OC	$O^{a,b}$		Broady (1984), Broady et al. (1987), Melick et al. (1991), Bargagli and Broady (1996)
	Nodularia harveyana				C^c	Fermani et al. (2007)
	Nostoc sp.		C			Bargagli and Broady (1996)
	Phormidium autumnale				O^d C^c	Fermani et al. (2007)

(continued)

Table 10.1 (continued)

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
	Phormidium fragile	OC	OC	OC*		Broady (1984), Broady et al. (1987), Bargagli and Broady (1996)
	Phormidium priestleyi				C^f	Fermani et al. (2007)
	Pseudoanabaena frigida				O^k	Izaguirre et al. (2006)
	Pseudoanabaena limnetica				O^k	Izaguirre et al. (2006)
	Schizothrix calcicola				C^f	Cameron and Benoit (1970)
	Synechococcus elongatus				C^k	Fermani et al. (2007)
	Tolypothrix boutelli was			O*		Broady et al. (1987)
Proteobacteria	*Klebsiella* sp.			C^a		Broady et al. (1987)
	Pseudomonas sp.				C^k	Cameron and Benoit (1970)
Diatoms						
Heterokontophyta	various				$O^{c,d,g,j}$	Fermani et al. (2007)
Fungi						
	“black mycelium yeast like”			C*		Zucconi et al. (1996)
	“yeast”	C				Ugolini and Starkey (1966)
	Mycelium sterile			C^a		Broady et al. (1987), Zucconi et al. (1996)
Ascomycota	*“Dematiaceae”*	C				Ugolini and Starkey (1966)
	Acremonium charticola			C^a		Zucconi et al. (1996)
	Aspergillus sp.	C		C^a		Broady et al. (1987), Zucconi et al. (1996), Ugolini and Starkey (1966)
	Cephalosporium sp.				C^f	Cameron and Benoit (1970)

(continued)

Table 10.1 (continued)

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
	Chaetomium sp.			C[a]		Zucconi et al. (1996)
	Fusarium sp.				C[f]	Cameron and Benoit (1970)
	Gliocladium sp.				C[f]	Cameron and Benoit (1970)
	Malbranchea pulchella va. Sulfurea			C[a]		Broady et al. (1987)
	Myceliophthora thermophile			C[a]		Broady et al. (1987)
	Neurospora	C				Ugolini and Starkey (1966)
	Paecilomyces sp.			C[a]		Broady et al. (1987)
	Penicillum sp.	C		C[a]	C[f]	Broady et al. (1987), Cameron and Benoit (1970), Ugolini and Starkey (1966)
	Engyodontium (Tritirachium) album				C[f]	(Cameron and Benoit 1970)
Basidiomycota	*“Basidiomycete”*				O[h]	Lewis-Smith (2005)
	Cryptococcus sp.			C[a]	C[f]	Broady et al. (1987), Cameron and Benoit (1970)
	Tritirachium roseum				C[f]	Cameron and Benoit (1970)
Zygomycota	*Mucor* sp.			C[a]		Broady et al. (1987)
Green algae						
Charophyta	*Klebsormidium dissectum*				C[k]	Fermani et al. (2007)
Chlorophyta	*Bracteacoccus minor*	OC				Broady (1984)
	Chlorella emersonii	C		C*		Broady et al. (1987)
	Chlorella protothecoides	C	C			Broady (1984), Bargagli and Broady (1996)

(continued)

Table 10.1 (continued)

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
	Chlorella reisigli	C				Broady (1984)
	Chlorella reniformis		C	C*		Broady et al. (1987), Bargagli and Broady (1996)
	Chlorella saccharophila	C				Broady (1984)
	Chlorellaceae				C^{g}	Fermani et al. (2007)
	Chlorococcum humicola				C^{f}	Cameron and Benoit (1970)
	Chlorococcum lobatum				$C^{c,k}$	Fermani et al. (2007)
	Chlorococcum sp.				C^{g}	Fermani et al. (2007)
	Chlorococcum tatrense				O^{c}, $C^{d,f,g}$	Fermani et al. (2007)
	Coccomyxa curvata	C				Broady (1984)
	Coccomyxa gloeobotrydiformis	C	C	C*		Broady (1984), Broady et al. (1987), Bargagli and Broady (1996)
	Sphaerocystis (Coenocystis) oleifera	C	C	OC*		Broady (1984), Broady et al. (1987), Bargagli and Broady (1996)
	Muriella zofingiensis				C^{g}	Fermani et al. (2007)
	Neospongiococcum vacuolatum				C^{c}	Fermani et al. (2007)
	Oocystis minuta	C	C			Broady (1984), Bargagli and Broady (1996)
	Pseudococcomyxa simplex	OC	OC	OC*		Broady (1984), Broady et al. (1987, Bargagli and Broady (1996)
	Scenedesmus sp.	C				Broady (1984), Lesser et al. (2008)
	Scotiellopsis terrestris	OC	C			Broady (1984), Bargagli and Broady (1996)

(continued)

Table 10.1 (continued)

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
	Tetracystis sp.				C^{j}	Fermani et al. (2007)
Lichen						
	"Lichenized alga"			O*		Broady et al. (1987)
	Caloplaca				C^{f}	Cameron and Benoit (1970)
	Xanthoria				C^{f}	Cameron and Benoit (1970)
Liverwort						
Marchantiophyta	*Cephaloziella exiliflora syn. C. varians*			O^{a}	O^{d,e,h,k}	Lewis-Smith (1984), Broady et al. (1987), Lewis-Smith (2005)
Moss						
Bryophyta	*Campylopus pyriformis*	O		O^{a}		Broady (1984), Broady et al. (1987), Lewis-Smith (2005)
	Pohlia nutans		O	O^{b}	O^{g,h,k}	Bargagli and Broady (1996), Bargagli et al. (2004), Lewis-Smith (2005))
Protozoa						
	Testatae rhizopods	O				Janetschek (1963)
Cercozoa	*Corythion dubium*			O^{a,b}		Broady et al. (1987)
Euglenophyta	*Spiromonas angusta*				C^{f}	Cameron and Benoit (1970)
Panarthropoda	Tardigrades	O				Janetschek (1963)
Rotifera	*Bdelloid rotifer*	O				Janetschek (1963)
Yellow-Green Algae						

(continued)

Table 10.1 (continued)

Division	Species	Mt. Erebus	Mt. Rittmann	Mt. Melbourne	Deception Island	References
Heterokontophyta	*Ellipsoidion stichococcoides*				C[k]	Fermani et al. (2007)
	Bumilleriopsis brevis				C[f]	Cameron and Benoit (1970)
	Xanthonema montanum				C[d,f,k]	Fermani et al. (2007)
	Xanthonema stichococcoides				C[c]	Fermani et al. (2007)

C cultured, *O* observed microscopically, [a] Cryptogram Ridge (Mt Melbourne), [b] NW Slope (Mt Melbourne), [c] Cerro Caliente (Deception), [d] Fumarole Bay (Deception), [e] West Stonebrow Ridge (Deception), [f] Telefon Bay (Deception), [g] Pendulum Cove (Deception), [h] Mount Pond (Deception), [j] Perchuc Cone (Deception), [k] Kroner Lake (Deception), [*] unclear in literature if data were for Cryptogram Ridge, NW Slope, or both each location (Skotnicki et al. 2001). However, it is unclear whether one site is the source for the other, or if they simply share a common off-continent source. The nearest known *C. pyriformis* is in the subantarctic South Sandwich Islands (Convey and Lewis-Smith 2006), while up to five other species of *Campylopus* are found on Deception Island (Lewis-Smith 2005). This species has a circumpolar distribution in the Southern Hemisphere and has also been documented in Western Europe, the Azores, and the United States (Corley and Frahm 1982; Stech and Wagner 2005).

Pohlia nutans has been recovered from the NW slope of Mt. Melbourne (Bargagli et al. 2004) and from Mt. Rittmann at temperatures of 17–35 °C (Bargagli and Broady 1996). Genetic characterization of both populations showed that they are closely related; however, as with *C. pyriformis*, they probably resulted from a single colonization event (Bargagli et al. 2004). The presence of *P. nutans* on the NW slope of Mt. Melbourne, but not at Cryptogram Ridge was suggested to be the result of a higher tolerance of *P. nutans* to the potentially toxic elements Cd, Pb, and Al (Bargagli et al. 2004). *P. nutans* has a circumpolar distribution in temperate and subarctic latitudes in both the Northern and Southern Hemispheres and is relatively common in the maritime Antarctic. It has been documented as a component of moss communities (both on heated and unheated ground) on Deception Island (Lewis-Smith 2005), as well as the South Sandwich Islands (Convey and Lewis-Smith 2006).

In the high-altitude sites, a single liverwort species, *Cephaloziella exiliflora* (syn. *C. varians*), has been observed at Mt. Melbourne (Broady et al. 1987). It is present at Deception Island mostly associated with heated ground (Lewis-Smith 1984, 2005), as well as the South Sandwich Islands (Convey and Lewis-Smith 2006), although it has been observed in non-heated ground at numerous subantarctic island, maritime, and coastal continental sites (Newsham 2010). *C varians* is globally distributed in mountainous regions and has been documented in the Arctic as *C. arctica* (Newsham 2010). In the maritime Antarctic and in Australia, *C. exiliflora* grows in association with mycorrhizal endophytes (Chambers et al. 1999); however, it has not been shown explicitly that the community of *C. exiliflora* at Mt. Melbourne also shares this trait. Various carotenoids and flavenoids, in particular riccionidin A, have contributed to the success of *C. exiliflora* in adapting to the cold temperatures and constant light in Antarctica, allowing it to be widely distributed (reviewed in Newsham 2010).

10.3.1.2 Algae

Three major lineages of eukaryotic algae have been observed at geothermal sites in Antarctica. Chlorophyta and Charophyta (green algae) are widespread, having been observed in every habitat examined, while Heterokontophyta (yellow-green algae and diatoms) have been observed only at Deception Island. Among the Chlorophyta, similar taxa are found in high-altitude geothermal areas, but no taxa found at these sites were found at Deception Island. It is unclear whether this difference in distribution of algal taxa is driven by altitude, latitude, geography, or due to errors in taxonomic identification. However, it is known that at each site, temperature is extremely important in structuring the growth of these organisms. For instance, there have been reports of substantial numbers of yellow-green algae and diatoms associated with subtidal fumaroles at Deception Island (Fermani et al. 2007); however, other studies indicate that these taxa are absent from samples specifically taken from higher temperature thermal features (Izaguirre et al. 2006). At Tramway Ridge, Mt. Erebus, green algae were recovered from all geothermal locations at a maximum temperature of 39 °C (Broady 1984).

Three chlorophyte species are found at all three high-altitude sites (Broady 1984; Broady et al. 1987; Bargagli and Broady 1996), but are also found in non-geothermal soils in northern Victoria Land (Cavacini 2001). These taxa include *Coccomyxa gloeobotrydiformis*, *Coenocystis oleifera* (*Sphaerocystis oleifera*), and *Pseudococcomyxa simplex*. *Coenocystis oleifera* was observed as a dominant member of reddish-brown felts covering soils and recorded as epiphytes on moss, at Mt. Melbourne (Broady et al. 1987), while *P. simplex* has been observed as dominant taxa in field specimens at both Mt. Melbourne and Tramway Ridge (Broady 1984; Broady et al. 1987), co-dominating with *Mastigocladus laminosus* (a cyanobacterium) at Mt. Melbourne, but preferentially growing at temperatures below 30 °C (Broady et al. 1987).

10.3.1.3 Fungi

There is limited information on fungi in the geothermal areas of Antarctica and what information exists, suggests that these organisms probably grow in the cooler fringes of geothermal features. Most of what we know regarding the distribution of fungi comes from cultivation studies, and early studies lacked crucial environmental temperature data (Table 10.1). Later studies did better in differentiating the temperatures at which samples were collected and from which fungi were cultured. On Mt. Melbourne, for instance, fungi were isolated from samples that were classified as “cool” moss material and hot soils (Broady et al. 1987; Zucconi et al. 1996). Merely being able to cultivate fungi from a particular sample, however, may not be sufficient proof that a given fungus is a member of the geothermal community. Numerous thermophilic and thermotolerant fungi have been isolated from areas in Antarctica distant from known geothermal features (Ellis 1980). Microscopic observation of fungi has occurred in only two studies, and in both cases, they were found in association with phototrophs in cooler areas. At Deception Island, an unknown Basidiomycete fungus was observed on Mt. Pond, associated with the moss *Dicranella hookeri* (Lewis-Smith 2005), while loosely lichenized algae were observed in cold areas at Mt. Melbourne (Broady et al. 1987).

10.3.1.4 Lichens

There is a blatant paucity of information on lichens associated with geothermal habitats and what information exists suggests that these composite organisms are restricted to cool areas around the periphery of warm soil. At Deception Island, *Caloplaca* and *Xanthoria* were recovered near young fumarolic soils as early colonizers (Cameron and Benoit 1970). At Mt. Melbourne, loosely lichenized algae were found in a dry, dark brown crust, and as an epiphyte on moss at locations with a surface temperature of 2 °C (Broady et al. 1987).

10.3.1.5 Protozoa

Protozoa have been found associated with mosses around the cooler areas near fumaroles. These locations are ideal for both mosses and their protozoan inhabitants because they provide liquid water and maintain warmer temperatures than nearby frozen areas. Protozoans are best enumerated from Deception Island; however, a few observations suggest that protozoa might also inhabit specific microniches at Mt. Melbourne and Mt. Erebus.

On Deception Island, protozoan colonization of “new” land created during the eruptions of 1967–1970 was studied over many years. The earliest published study found *Spiromonas angusta* co-cultured with algae from the newly formed fumarolic soils from the December, 1967 eruption (Cameron and Benoit 1970). Soil temperatures of these samples were never given; however, from sample descriptions, it is inferred that they came from the proximity of actively degassing, heated fumaroles. Subsequently, a thorough multi-year characterization of protozoan colonization of volcanic tephra was carried out (Smith 1974, 1985). In this long-term study, soil temperature was also not reported. In the earlier publication, only two areas (New Island, Eruption Center) could have possibly possessed geothermal habitats and all protozoans observed in these two areas were also observed in samples obtained from known non-geothermal habitats (Cathedral Crags and Collins Point) (Smith 1974). The latter publication expanded the study to include moss samples collected from Fumarole Bay; however, fumaroles in Fumarole Bay are generally in the intertidal zone, devoid of mosses, and therefore, these samples almost certainly came from non-geothermal habitats (Smith 1985).

Reports of protozoa from geothermal habitats in Victoria Land are few. On Mt. Erebus, observations of protozoa are from Tramway Ridge exclusively and include a small, colorless bdelloid rotifer, testate rhizopods and possibly Tardigrades, as evidenced by an old cyst (Janetschek 1963). Later studies at Tramway Ridge, however, failed to uncover any evidence of protozoa (Broady 1984). There has been no further verification of Tardigrades or rotifers associated with geothermal habitats in Antarctica, whereas a single testate rhizopod, *Corythion dubium*, has been observed at Mt. Melbourne as empty tests in mesothermal soils, within mineral substrata or associated with bryophytes (Broady et al. 1987).

This species is generally associated with non-geothermal bryophytes in Dronning Maud Land, Victoria Land (Smith 1992), and in the maritime Antarctic (Smith 1974, 1985), including several non-geothermal habitats on Deception Island (Smith 1985).

10.3.2 Prokaryotes

Over the last 30 years, prokaryotes have been studied in Antarctic geothermal locations using a variety of techniques. Until recently, relatively few phyla have been reported for these habitats. Cyanobacteria and Firmicutes have been well characterized at each location due to the ability to study them using traditional culture-dependent techniques. More recently, molecular methods have been employed to examine the community structure at these locations and are revealing the presence of numerous potentially endemic lineages that so far have evaded detection using more traditional techniques.

10.3.2.1 Cyanobacteria

Cyanobacteria, like moss and algae, exhibit conspicuous zonation patterns related to temperature and pH gradients (Broady 1984; Broady et al. 1987; Bargagli and Broady 1996; Bargagli et al. 2004; Soo et al. 2009). In a similar fashion to the way that algae are distributed among the different geothermal sites, the microbial communities at the three high-elevation geothermal sites in Victoria Land share many cyanobacterial taxa that are minor members, or are absent, from cyanobacterial populations at Deception Island (Table 10.1). The two most conspicuous mat-forming species of cyanobacteria at Tramway Ridge, Mt. Melbourne and Mt. Rittmann are *Phormidium fragile* and *Mastigocaldus laminosus*.

At Tramway Ridge, *P. fragile* was the dominant taxon in red-brown felts with a blue-green undersurface that dominate the temperature range of 30–40 °C, but was also observed as part of crusts from as low as 10 °C (Broady 1984). *P. fragile* was found at Mt. Melbourne at low levels over a wide temperature range, but was not as dominant as at Tramway Ridge (Broady et al. 1987). At Mt. Rittmann, *P. fragile* was observed rarely in samples but grew readily in media incubated at 20 or 40 °C (Bargagli and Broady 1996).

Mastigocladus laminosus has been observed microscopically as the dominant cyanobacterial species from Mts. Rittmann, Melbourne, and Erebus and has been cultivated from Mt. Erebus (Broady 1984; Broady et al. 1987; Bargagli and Broady 1996). At least two distinct strains of *M. laminosus* can be found in Antarctic geothermal locations. Strain ENH is the dominant taxon in dark gray to black felt mats found at temperatures between 40 and 60 °C (Broady 1984) and appears to be endemic to Tramway Ridge. It can be differentiated from the more widespread strain EH because it is generally unbranched, lacks heterocysts, and seems to occupy slightly higher temperatures in field observations (Broady 1984; Broady et al. 1987; Melick et al. 1991). These properties originally caused strain ENH to be misidentified as *Lyngbya* sp. (Broady 1984; Broady et al. 1987). Strain ENH was found to be tolerant to a wide regime of desiccation and freezing treatments (Melick et al. 1991), surviving more than 120 days being either frozen in the dark, or incubated at 50 °C in the light. Interestingly, it is not viable after 42 days frozen under constant light, or incubated at 50 °C in the dark. These constraints suggest that this organism survives the 4 months of dark winter as frozen propagules and must recolonize fumaroles each Antarctic Spring (Melick et al. 1991).

Photosynthetic rates were measured in cultured *M. laminosus* strain ENH, *P. fragile,* and *P. simplex*. These three organisms had considerable overlap in being capable of photosynthesis over a wide range of temperatures, however, were shown to prefer specific temperature ranges (Melick et al. 1991). *M. laminosus* strain ENH was found to be active at the highest temperature (42–44 °C) of these organisms, followed by *P. fragile* (34–36 °C), and then *P. simplex* (24–30 °C), an apparent temperature-based selection pressure that describes zonation observed in the field (Broady 1984; Melick et al. 1991). Interestingly, in the field, *M. laminosus* strain EH and *M. laminosus* strain ENH were reportedly never observed in the same sample, even though conditions were amenable to either strain occurring (Broady 1984; Melick et al. 1991). The mechanism driving this microbiogeography remains unclear.

10.3.2.2 Proteobacteria

Only two proteobacteria have been reported from geothermal habitats in Antarctica, and details regarding their isolation and characterization are severely lacking. *Klebsiella* sp. were reportedly cultured from Cryptogram Ridge, Mt. Melbourne, but were not thoroughly characterized (Broady et al. 1987), while *Pseudomonas* sp. were reported as a member of freshly formed fumarolic soils on Deception Island (Cameron and Benoit 1970).

10.3.2.3 Firmicutes

As would be expected, spore-forming Firmicutes, in particular bacilli, have been isolated from every geothermal environment studied in Antarctica (Table 10.1) (Ugolini and Starkey 1966; Cameron and Benoit 1970; Bargagli and Broady 1996; Broady et al. 1987). Many of these have been validly identified and phenotypically characterized, while others are only identified as "*Bacillus* sp." (Cameron and Benoit 1970; Nicolaus et al. 1991). This is unsettling given that many of the organisms originally identified as "*Bacillus* sp." that were studied and maintained in culture collections have since been reassigned from the genus *Bacillus* into other genera, such as *Alicyclobacillus* (Wisotzkey et al. 1992) and *Geobacillus* (Nazina et al. 2001; Coorevits et al. 2012). More recent cultivars include members of the genera *Brevibacillus*, *Aneuribacillus,* and *Anoxybacillus*. Clostridia have been reported from Tramway Ridge as "glycolytic anaerobes" but none have yet been fully characterized and formally classified (Hudson and Daniel 1988).

Geobacillus thermantarcticus was first isolated as an unnamed *Bacillus* sp. from Cryptogram Ridge, Mt. Melbourne (Nicolaus et al. 1991). As a "*Bacillus* sp.," it was included in a study of polar lipid composition changes in relation to growth temperature and, like other thermotolerant bacilli in the study, it was found to adapt by adding fatty acids with higher melting points to its membrane (Nicolaus et al. 1995). This organism was later fully characterized and named *Bacillus thermoantarcticus* (Nicolaus et al. 1996). It has been the subject of many studies aimed at characterizing xylan utilization pathways (Lama et al. 2001, 2004, 1996; Çalık et al. 2009), exopolysaccharides (Manca et al. 1996), sensitivity to heavy metals (Poli et al. 2009), secreted protease (Dipasquale et al. 2008), and ADP-ribosylation reaction (Faraone-Mennella et al. 2006). Its membrane adaptations to changing temperature have also been studied (Nicolaus et al. 2001). It is physiologically and genetically similar to *Geobacillus thermoglucosidasius*, but differs sufficiently to be considered a novel species (Nazina et al. 2001; Nicolaus et al. 1996; Zeigler 2005). Finally, in 2012, *B. thermantarcticus* was officially proposed to be moved to the genus *Geobacillus* (Coorevits et al. 2012).

Alicyclobacillus pohliae was isolated from soil collected on the NW slope of Mt. Melbourne near the shoots of the moss, *Pohlia nutans* (Bargagli et al. 2004) and fully characterized later (Imperio et al. 2008). *A. pohliae* is facultatively anaerobic, requires soluble iron for growth (Pepi et al. 2005), and appears to grow best in aqueous media derived from its home soil, suggesting possible geochemical controls on its habitat range (Pepi et al. 2005).

Alicyclobacillus acidocaldarius was isolated from Mt. Erebus (Hudson and Daniel 1988) (Hudson et al. 1989) and Mt. Rittmann (Nicolaus et al. 1998). Three isolates were further characterized and classified as *B. acidocaldarius* (Hudson et al. 1989), later re-evaluated and named *A. acidocaldarius* (Wisotzkey et al. 1992); however, this later study did not include the Antarctic isolate specifically. *A. acidocaldarius* subsp. *rittmannii* was isolated from Mt. Rittmann from samples collected during 1993/1994 (Nicolaus et al. 1998) and has since been used in biochemical studies of thermophilic enzymes. Its β-galactosidase was purified and determined to have an optimum temperature of 65 °C and optimum pH of 6.0, slightly higher in both temperature and pH than other strains of *A. acidocaldarius* (Gul-Guven et al. 2007, 2011).

Anoxybacillus amylolyticus is a facultative anaerobe isolated from soil collected from Mt. Rittmann in 2002/2003 (Poli et al. 2006). It has been shown that *A. amylolyticus* from Mt. Rittmann secretes less α-amylase when grown in high metal concentration conditions, in particular Hg^{2+} (Poli et al. 2009). This observation was used to suggest that mercury concentrations may play a role in determining the different distributions of bacilli observed over the three continental volcanoes.

Aneurinibacillus terranovensis and *Brevibacillus levickii* were isolated from samples collected during the 11th and 14th Italian Antarctic Expeditions (1995–1996 and 1998–1999) (Logan et al. 2000). They were cultivated from different areas, using similar isolation conditions: *A. terranovensis* was cultivated only from Cryptogram Ridge, Mt. Melbourne and Mt. Rittmann, while *B. levickii* was cultivated only from the NW slope of Mt. Melbourne (Logan et al. 2000; Allan 2005). Both species grow over a similar range of temperature (15–55 °C) and pH (3.5–6.5). Minor differences include that *A. terranovensis* is microaerophilic and weakly catalase-positive, and *B. levickii* has a higher uptake rate of glutamate and a preference for nutritionally richer media (Allan 2005).

10.3.2.4 Actinobacteria

Actinobacteria have been cultivated from soil collected from Tramway Ridge, Mt. Erebus (Broady et al. 1987; Nicolaus et al. 1992), Cryptogram Ridge and the NW slope of Mt. Melbourne (Broady et al. 1987; Bargagli et al. 2004), and Deception Island (Cameron and Benoit 1970). Thermophilic *Micrococcus* sp., *Streptomyces coelicolor,* and *Thermomonospora* sp. were isolated from Cryptogram Ridge, Mt. Melbourne, but the details of their identification and characterization were underreported (Broady et al. 1987). *S. coelicolor* and *Thermomonospora* sp. were also isolated from Tramway Ridge, Mt. Erebus (Broady et al. 1987); however, the effort was never published in a peer-reviewed journal. From Deception Island, *Corynebacterium* sp., *Mycobacterium* sp., *Nocardia* sp., and *Micrococcus* sp. were reportedly isolated from fumarolic soils, but again, details of their characterization are lacking (Cameron and Benoit 1970). Mesophilic *Micrococcus* sp. strains isolated from near Tramway Ridge, and from Cryptogram Ridge on Mt. Melbourne, were specifically noted for their halotolerance (Nicolaus et al. 1992) and were further studied for lipid composition responses to different environmental salinity (Nicolaus et al. 2001).

10.4 Molecular Research

Molecular genetic characterization of Antarctic geothermal microbial communities has only been reported in three studies, which all focused on subsurface prokaryotes. Unfortunately, comparing these studies has been difficult because they use different molecular methodologies and were focused on different target communities. Two studies were undertaken on subsurface communities inhabiting Tramway Ridge, Mt. Erebus (Soo et al. 2009, while another study focused on a subtidal fumarole at Deception Island (Muñoz et al. 2011). Despite these differences, the studies all agree that the geothermal habitats of Antarctica are vastly

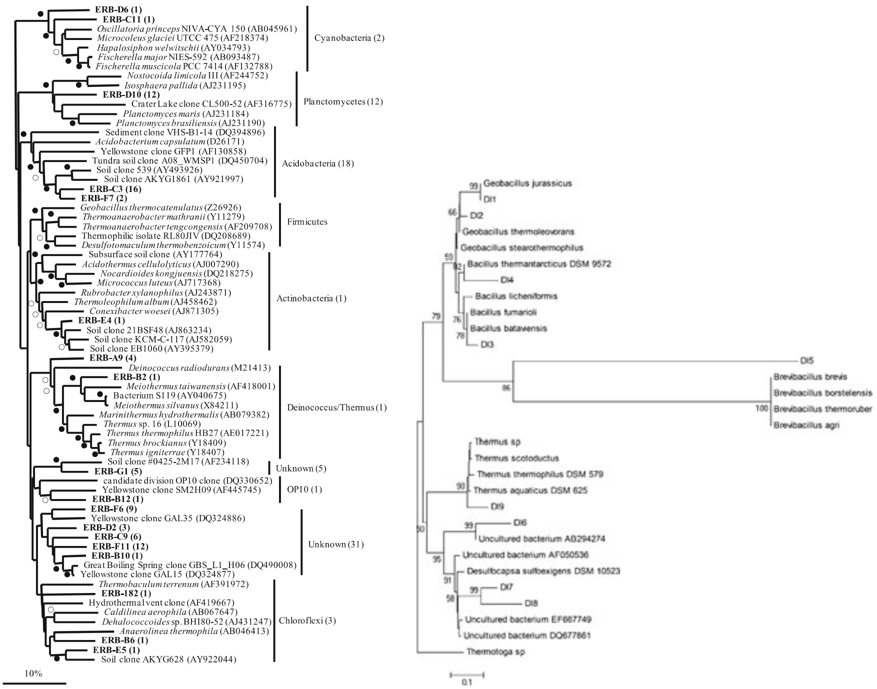


Fig. 10.7 *Left* phylogeny from Soo et al. (2009) showing diversity of taxa encountered at Tramway Ridge and recovered using molecular techniques. *Right* phylogeny from Munoz et al. (2011) showing diversity of taxa encountered in Fumarole Bay, Deception Island

more diverse than suggested by cultivation and microscopy-based studies. Whereas cultivation implied that Firmicutes play key ecological roles in geothermal environments, molecular studies now suggest that these taxa are probably vastly outnumbered by other prokaryotes that are simply difficult to isolate using cultivation techniques. Clearly our understanding of the microbial community at these locations is in its infancy, and there is much work to be done before we can be confident that we understand the composition, much less functional capabilities of microorganisms in these environments.

A study conducted at an intertidal fumarole located in Fumarole Bay, Deception Island, used a DNA fingerprinting tool (Denaturing Gradient Gel Electrophoresis—DGGE) to examine bacterial diversity (Muñoz et al. 2011). Nine bands from the gel were sequenced. While five of these best-matched different types of bacilli, three were identified as sulfate-reducing delta-proteobacteria, and one was identified as Thermus/Deinococcus group (Fig. 10.7). At this point in time, this is the only published study on Deception Island geothermal habitats using molecular methods.

At Tramway Ridge, a study using automated ribosomal intergenic spacer analysis (ARISA) was undertaken to examine the diversity of bacteria and cyanobacteria over the lateral pH/thermal gradient near steam fumaroles (Soo et al. 2009). The general bacterial diversity was lowest in the hottest sites and highest in the coolest sites, while no difference in cyanobacterial diversity was observed over the gradient. Both the bacteria and cyanobacteria at Tramway Ridge formed two types of community, with the hottest sites sharing a community, and all other samples sharing a common community, despite which fumarole was sampled. The environmental variables that were found to be most influential over community similarity were temperature, pH, and moisture content for bacteria. Cyanobacterial diversity, however, was found to be correlated to temperature, pH, total carbon, Ca, and Li. Bacterial and archaeal clone libraries of nearly full-length small-subunit ribosomal ribonucleic acid (SSU-rRNA) genes from one of the hottest samples at Tramway Ridge were also constructed in this study. Analysis of full-length SSU-rRNA genes suggests that Acidobacteria, Planctomycetes, Chloroflexi, OP10/Armatimonadetes, and many unclassified taxa are probably the dominant bacteria in the subsurface (Fig. 10.7). Sequences corresponding to the conspicuous mat-forming cyanobacteria, *M. laminosus*, known to dominate the surface of Tramway Ridge, were observed, but only as chimeric sequences (Namsaraev et al. 2011). In contrast to cultivation studies, no Firmicutes and only one actinobacterial sequence were observed. Archaea observed in this study were members of Group 1.1b of the Thaumarchaeota.

Building from the Soo et al. (2009) study, the communities inhabiting the hottest (65 °C) fumarolic soils at Tramway Ridge were examined using partial SSU-rRNA amplicons and full-length SSU-rRNA sequences reconstructed from environmental shotgun metagenomics (Herbold et al. 2013—submitted manuscript).

Whereas the previous study was focused on the differences in community composition between soil samples with different pH and temperature, this later study was focused on determining community differences between samples that have nearly identical temperature and pH, but were taken from different depths within fumaroles. It was found that extractable DNA per gram of soil was much higher in the surface (0–2 cm depth) than in deeper substrata (2–4 and 4–8 cm). The surface layer also had a substantial amount of DNA derived from taxa whose closest relatives are mesophiles, many of which are globally distributed and common organisms in soils elsewhere on the planet. The deeper substrata on the other hand were found to be dominated by a highly divergent archaeon that was completely absent in earlier datasets, and a Planctomycete, for which Soo et al. (2009) reconstructed a nearly full-length sequence. Other taxa that were prominent in the subsurface include several lineages of thermally restricted organisms and candidate divisions for which very little knowledge exists. Yet, the sequences observed at Tramway Ridge bear a high identity to sequences at Yellowstone National Park (USA) and el Tatío Geyser Field (Chile).

Aeolian transport has been invoked to explain the presence of genetic signatures for globally distributed taxa at Tramway Ridge; however, the fact remains that there seem to be organisms there that do not exist elsewhere on Earth. Tramway Ridge, we hypothesize, is a community that is currently dominated by a few "endemic" organisms but that also hosts a large population of recent immigrants. This, of course raises interesting ecological questions regarding succession and community dynamics over time.

10.5 Summary

Geothermal habitats in Antarctica are restricted to volcanic areas, four of which are known to possess these habitats. Three (Mts. Erebus, Melbourne, and Rittmann) are located in Victoria Land, and one (Deception Island) is located in the South Shetland Islands. The three Victoria Land volcanoes are south of the Antarctic Circle and geothermal habitats at these locations exist at high altitude (>2,400 m). Deception Island on the other hand is north of the Antarctic Circle, and geothermal habitats are located at low altitude (<540 m). These obvious geographical differences are reflected in distributions of bryophytes, algae, and cyanobacteria, for which there are common taxa shared between the volcanoes of Victoria Land, and a completely different and more diverse assemblage found at Deception Island.

Temperature and pH seem to be largely responsible for local spatial organization of organisms at geothermal sites; however, there are probably additional geochemical controls on organization. The two geothermal areas on Mt. Melbourne (Cryptogram Ridge and NW slope) have been found to host different species of moss and bacilli, and these different species were found to have slightly different nutritional requirements. The fact that these two areas are close to one another, and presumably subject to the same colonization events, suggests local geochemical controls over community composition.

Most of our understanding of Antarctic geothermal systems comes from microscopic investigation and cultivation work. What is abundantly clear from the molecular work accomplished to date are the glaring gaps in knowledge that still exist. Molecular studies have been centered on a few fumaroles at Tramway Ridge and a single subtidal fumarole at Deception Island. The studies on Tramway Ridge have reinforced observations that temperature and pH are important factors in determining community composition, have expanded our knowledge of the taxonomic composition by at least one, if not two, orders of magnitude, and revealed a rich, hidden ecosystem of abundant and novel lineages. Molecular work suggests that in the subsurface of Tramway Ridge, endemic archaea and not bacteria predominate. Furthermore, over the next few years, similar studies at Mt. Melbourne, Mt. Rittmann and Deception Island will be published, further revealing the similarities and differences between these geothermal habitats.

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Chapter 11
Microbial Life in Antarctic Permafrost Environments

Jacqueline Goordial and Lyle Whyte

Abstract Permafrost is extensively distributed throughout terrestrial Antarctica, and contains soils that are the oldest, coldest, and driest on Earth. Currently, relatively little is known about the microbial life in Antarctic permafrost compared to its Arctic and Alpine permafrost counterparts. However, a growing body of evidence indicates that the Antarctic permafrost microbial community can be as diverse as those found in the Arctic, but soils have several orders of magnitude less biomass. Similar phyla of bacteria (Firmicutes, Actinobacteria, Bacteriodetes) are found and isolated in permafrost from both poles, and evidence to date from the Arctic indicate that permafrost is a habitable environment, in spite of the extreme cold, oligotrophy and low water activity associated with the soils. Of special interest in the Antarctic is the presence of dry permafrost soil that remains below 0° C and contains negligible amounts of water; such permafrost environments are found in the upper elevations of the McMurdo Dry Valleys, the only place on Earth where dry permafrost is known to occur. It is currently not known if active microbial communities can exist in such hyper-arid dry permafrost soils, and Antarctic permafrost in general. Questions that remain to be answered include whether permafrost microbial communities are active or viable in situ, or whether they represent cryopreserved fossils. If viable, what are the adaptations that allow life to be sustained over geologic timescales in permanently subzero environments? And finally, are the cold and arid limits of microbial life found in the Dry Valley permafrost soils of the Antarctic?

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11.1 Introduction

Antarctic environments, such as sea ice, glacial ice, lakes, streams, and even rocks (endoliths and hypoliths), have recently been recognized to contain habitable niches which harbor active and diverse microbial communities (de la Torre et al. 2003; Bowman et al. 1997; Murray et al. 2012; Lauro et al. 2011; Mikucki and Priscu 2007). Terrestrial Antarctic surface soils, including Dry Valley soils, were initially believed to be sterile and inhospitable for life (Horowitz et al. 1969, 1972) but are now known to host diverse and significant microbial biomass (Lee et al. 2012; Cowan et al. 2002). In comparison with other Antarctic environments, however, relatively little is known about the microbial diversity, activity, and ecology existing within Antarctic permafrost, despite the fact that 37 % of all of the world's permafrost exists throughout the $\sim$280,000 km^2 ice-free regions of the Antarctic (Bockheim 1995; Bockheim and Hall 2002). Permafrost is considered an extreme cryoenvironment where indigenous microorganisms must survive prolonged exposure to subzero temperatures and background radiation for geological timescales in a habitat with low water activity and extremely low rates of nutrient and metabolite transfer (Steven et al. 2006).

In spite of the hostile conditions of permafrost, substantial amounts of microbial biomass are found in Arctic permafrost, and there is a growing body of evidence that viable cells are metabolically active in Arctic permafrost at ambient subzero temperatures (-15 to -25 °C) (Rivkina et al. 2000; Mykytczuk et al. 2013). As of 2013, however, investigations into the prokaryotic component of Antarctic permafrost are limited to four studies: Cameron and Morelli (1974), Gilichinsky et al. (2007), Blanco et al. (2012), and Tamppari et al. (2012). The earliest study investigated the viability of Antarctic permafrost microorganisms by classical, culture-dependant methodologies. However, the authors were not able to demonstrate that the obtained cultured microorganisms were indigenous to permafrost because of possible contamination from drill fluids used to obtain permafrost cores (Cameron and Morelli 1974). Fluid-less permafrost-drilling techniques (Blanco et al. 2012; Gilichinsky et al. 2007) or sampling ice-cemented ground with a hammer and chisel (Tamppari et al. 2012) were recently employed in microbiological studies in the Antarctic. However, knowledge of the habitability of permafrost remains primarily informed by investigations from Arctic and Alpine regions. The limited work done on Antarctic permafrost, when compared with surface soils, is mainly due to the considerable logistical challenges and very high costs associated with obtaining non-contaminated permafrost samples through permafrost drilling from the very remote regions of Antarctica.

11.1.1 Antarctic Permafrost Environments

Permafrost, defined as soil which remains below 0 °C for at least two consecutive years, is typically overlain with an 'active layer' that seasonally rises above 0 °C and which can extend several meters down. Active layer's thickness and depth to ice-cemented permafrost in the Antarctic is heterogeneous and is influenced by regional climate, proximity to glaciers, age, the presence of vegetation, snow cover, and surface albedo. Active layer soils occur in the ice-free regions of the Antarctic peninsula, offshore islands, and maritime Antarctica (Bockheim 1995; Bockheim and Hall 2002). The McMurdo Dry Valleys (MDVs) in inland Antarctica are a particularly harsh and low water activity permafrost environment, characterized by hyperaridity in addition to the cold. Moisture content is extremely low (<5 %), and dry permafrost forms from sublimation of moisture in ice-cemented permafrost over time. The Dry Valleys are the only place on Earth where a layer of dry soil overlays ice-cemented ground permafrost (Mckay 2009) and, at high elevations, entirely lack an active layer which rises above 0 °C (Marinova et al. 2013). Water exchanges between the dry soil and ice-cemented permafrost via vapor diffusion rather than liquid water. Despite being in the vapor phase, this water is thought to be available to microbial cells (Stomeo et al. 2012).

Polygon-patterned ground is commonly found in permafrost affected terrain (Fig. 11.1). Depressions forming the polygon boundaries are underlain with V-shaped ice wedges and are found throughout the ice-free regions of the Antarctic (Bockheim and Hall 2002). In the Dry Valleys where dry surface soils predominate, the trough-like depressions may be underlain by sand wedges instead of ice, though ice veins and ice lenses may also be found within sand wedge structures (Bockheim et al. 2009). The microbiology of ice wedges and sand wedges in Antarctic polygon terrain remains unexplored. Work on young (~4,000 years) and old (~25,000 year old) ice wedges in the Arctic indicates that these are habitable cryoenvironments which contain up to 10^6–10^8 cells/g culturable microorganisms and show evidence of in situ heterotrophic activity based on occluded gas measurements (Wilhelm et al. 2012a; Katayama et al. 2007; Lacelle et al. 2011).

11.1.2 Habitability of Permafrost Environments

In addition to the extreme cold and often oligotrophic conditions, one of the primary constraints to microbial life in permafrost is the lack of liquid water. Liquid water could be present in ice-cemented ground in small amounts, despite the subzero temperatures. Concentrated solutes in frozen soils can reduce the freezing point of water causing the presence of briny veins within permafrost (Anderson 1967). The ordering effects of clay minerals are also known to stabilize liquid water into very thin films adsorbed to the mineral grain and may be the only

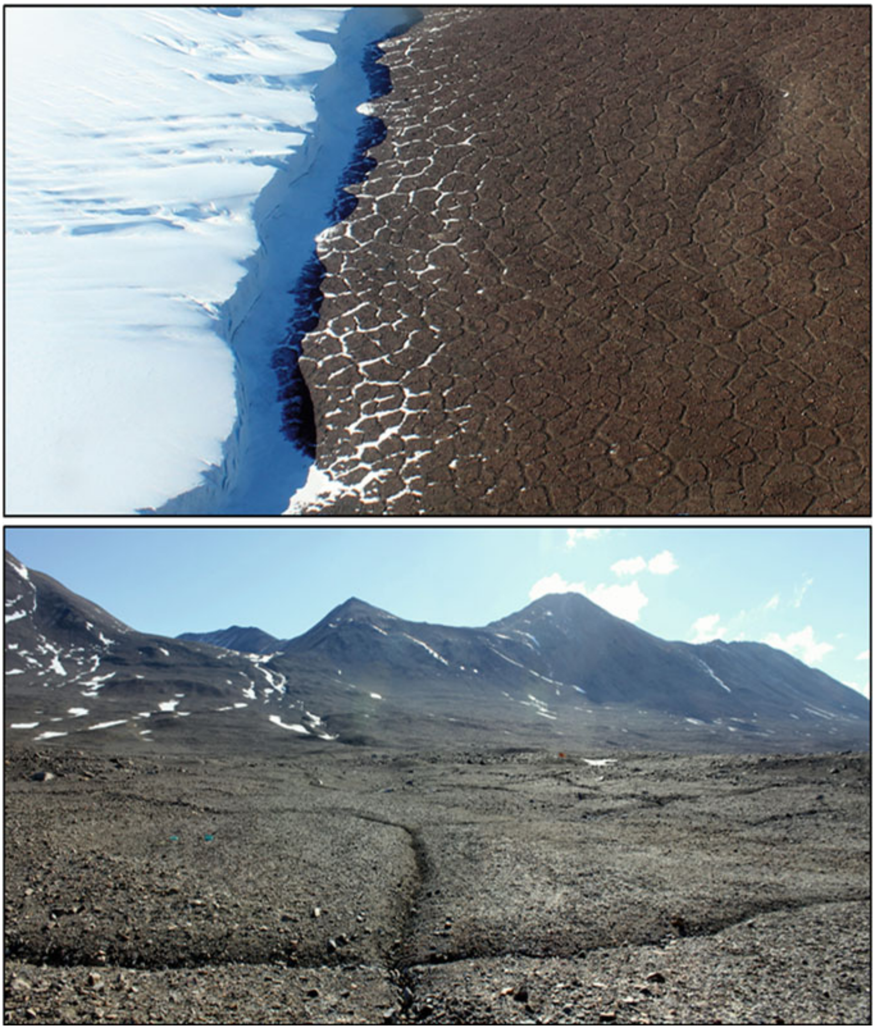

Fig. 11.1 Polygon-patterned permafrost in the Antarctic. polygon-patterned ground in the McMurdo Dry Valleys, aerial view (*top*), and view from the ground (*bottom*)

available water at subzero temperatures (Anderson 1967; Jakosky et al. 2003). In the Dry Valleys, the interface between dry permafrost and ice-cemented permafrost may also be habitable, if water vapor exchanging between the ice-rich permafrost and overlying dry regolith soils is available to microorganisms.

Nutrient content in permafrost soils in the Antarctic is heterogeneous. Soils in Antarctica are generally oligotrophic, though soils in close proximity to available water (lakes and streams), ornithographic soils, and coastal Antarctic soils have higher-organic C content. The source of organic carbon and nitrogen in Antarctica may originate from aeolian deposition of organic matter from modern or ancient lacustrine, marine, or lithic sources (Burkins et al. 2000; Hopkins et al. 2009; Cowan et al. 2011). Carbon and nitrogen isotopic signatures that are indicative of primarily ancient aquatic sources of organics, rather than reflective of wind deposition from modern sources, were found in one Dry Valley (Burkins et al. 2000). However, the total contribution of ancient carbon to Antarctic soils and permafrost remains unknown (Hopkins et al. 2009).

Relative to Arctic permafrost, very few studies have investigated the microbiology of Antarctic permafrost. Much of what is known about soil microbiology in the Antarctic is currently derived from investigations of surface active soils, and mostly from Dry Valley soils. This small but increasing body of research indicates that similar amounts of microbial biomass are present in Antarctic surface soils (10^6–10^8 cells/g wet soil) as reported for temperate soil habitats, and also high levels of microbial diversity (Lee et al. 2012; Cowan et al. 2002). Taking into account the very few Antarctic permafrost samples analyzed, it appears that relatively low amounts of microbial biomass are present in Antarctic permafrost samples (10^3–10^4 cells/g wet soil) compared with Arctic regions (10^5–10^8 cells/g wet soil) (Table 11.1), and the abundance of microbial cells reported in Dry Valley and coastal permafrost generally decreases with depth (Blanco et al. 2012; Gilichinsky et al. 2007).

11.1.3 Molecular Microbial Diversity

Molecular surveys of diversity in permafrost showed the presence of aerobic and anaerobic microorganisms, with similar phyla detected in Antarctic and Arctic permafrost. In both cases, there is a predominance of phylotypes belonging to Actinobacteria, Proteobacteria, Firmicutes, and Bacteriodetes (Gilichinsky et al. 2007; Steven et al. 2007; Hinsa-Leasure et al. 2010; Yergeau et al. 2010); it is likely that these bacteria are selected for in permafrost environments. For example, spore-forming Bacteriodetes and Firmicutes may be better adapted to resist the permanently frozen conditions of permafrost. Some Actinobacteria show metabolic activity at subzero temperatures (Katayama et al. 2009; Christner 2002) and also may be protected in the permafrost environment by cyst-like resting forms as observed in *Arthrobacter* and *Micrococcus* species (Soina et al. 2004). Overall, at least 11 phyla have been detected in Antarctic permafrost using molecular methods to date (Table 11.2). The source of such diversity is likely to be related to the overlying surface soils, atmospheric deposition of bacteria, nearby colonized habitats such as hypoliths, cryptoendoliths, and microbial mats from colonized streams and lakes (Pearce et al. 2009; Pointing et al. 2009). For example, in Dry Valley permafrost, Gilichinsky et al. (2007) reported that 16S rRNA phylotypes found in surface soils were closely related to those in the underlying ice-cemented permafrost. Nonetheless, the sources and extent of microbial diversity found in Antarctic permafrost remain very poorly characterized.

Table 11.1 Microbial biomass in permafrost environments

Location	Age of permafrost (years)	Microbial functional groups reported	Viable cell counts	Direct microscopic cell counts	Reference
Antarctic Dry Valley permafrost Taylor Valley, Miers Valley, Beacon Valley, Mount Feather	30,000–8 million	Aerobic heterotrophs Methanogens Sulfate Reducers Denitrifiers	$0–10^4$ $2–10^1$ $0–10^3$ $0–10^1$	10^5	Gilichinsky et al. (2007)
Antarctic Dry Valley permafrost University Valley	2,500–120,000	Aerobic heterotrophs	0–6	10^3	Goordial (unpublished)
Antarctic peninsula permafrost Deception Island	200	Aerobic heterotrophs	$0–10^5$	n.d.	Blanco et al. (2012)
Canadian high Arctic permafrost Eureka	5,000–6,000	Aerobic heterotrophs	$10^1–10^4$	10^8	Steven et al. (2007, 2008)
Canadian high Arctic ice wedge Axel Heiberg	>4,000	Aerobic heterotrophs Ammonia oxidizing Archaea Denitrifiers	$10^4–10^5$	10^8	Wilhelm et al. (2012b)

Table 11.2 Bacterial phyla found in permafrost

Phylogenetic group	Antarctic dry valley permafrost[a]	Antarctic peninsula permafrost[b]	Dry valley soils[c]	Permafrost interface in maritime-influenced dry valley[d]	Maritime dry valley soils[d]	Maritime Antarctic soils[e]	Continental Antarctic soil[e]	Canadian high arctic permafrost[f]
Acidobacteria	+	+	+	+	+	+	+	+
Actinobacteria	+	+	+	+	+	+	+	+
Armatimonadetes (formally OP10)						+		
Bacteriodetes		+	+	+	+	+	+	+
Chlorobi				+	+			
Chloroflexi	+	+	+			+		
Cyanobacteria		+		+	+	+	+	
Deinococcus-Thermus		+	+		+			
Fibrobacteres	+							
Firmicutes	+	+	+	+	+	+		+
Fusobacteria						+		
Gemmatimonadetes		+	+	+		+		+
Nitrospira			+					
Plantomycetes		+			+	+	+	+
Proteobacteria	+	+	+	+	+	+	+	+
Spirochetes					+			
TM7		+						
Verrumicrobia				+		+	+	

[a] Gilichinsky et al. (2007), [b] Blanco et al. (2012), [c] Lee et al. (2012), [d] Stomeo et al. (2012), [e] Yergeau et al. (2010), and [f] Steven et al. (2007)

In addition to prokaryotes, algae, yeast, and fungi have been found in permafrost (Zucconi et al. 2012; Kochkina et al. 2012; Gilichinsky et al. 2007). The relative contribution of Archaea in Dry Valley permafrost soils is not well known, with multiple studies finding no Archaea using current molecular methodology (Farrell and Pointing 2010; Lee et al. 2012). Gilichinsky et al. (2007) were able to detect methane production from cultured samples of Dry Valley permafrost but did not identify the Archaea in the samples. We also recently detected Archaea (methanogens and halobacteria) in permafrost from University Valley (UV), in the Upper Dry Valleys (Goordial unpublished).

11.1.4 Culturable Microbial Diversity

It is widely recognized that culturable microorganisms represent less than 1 % of the microbial population in soils, and in permafrost, the culturable proportion may be even lower; culturable bacteria from permafrost in the Arctic and Antarctic represent <0.1/0.01 % of the bacteria identified in samples using molecular methods (Gilichinsky et al. 2007; Steven et al. 2007). In general, culturing permafrost bacteria on low-nutrient media such as R2A has yielded the most isolates. However, increased representation of culturable microorganisms has been obtained by alternative methods such as thawing permafrost samples at high temperatures (52 °C) (Kochkina et al. 2012) and incubating natural samples at the 'warm' temperature of 5 °C prior to plating (Vishnivetskaya et al. 2000). Monitoring permafrost samples over time using this method with DAPI staining revealed that cell numbers increased in the sample, while numbers of CFU did not, suggesting that there is a proportion of viable microorganisms in permafrost that are not amenable to the culturing methodologies being currently employed. Antarctic permafrost bacteria isolated and characterized have mostly been identified as psychrotrophs rather than true psychrophiles, indicating that these microorganisms may represent a community of 'survivors' rather than organisms which thrive in these environments. Microorganisms isolated and identified to date from Antarctic permafrost are outlined in Table 11.3 and include a small number of representatives from the Actinobacteria, Proteobacteria, Bacteriodes, and Firmicutes. Many of the genera isolated from Antarctic permafrost have also been identified in Arctic permafrost indicating that such organisms are particularly adapted to survive in such harsh cyroenviroments.

11.2 Microbial Activity

While nitrate reducers, methanogens, and sulfate reducers have been detected in Dry Valley permafrost, it is still unknown whether they are metabolically active in situ (Gilichinsky et al. 2007). It is noteworthy to add that the enzymes

Table 11.3 Phyla and genera of Bacteria cultured from Antarctic permafrost

Phylogenetic group	Antarctic dry valley permafrost[a]	Antarctic peninsula permafrost[b]	Dry valley soil[c]	Antarctic coastal high-elevation soil[d]	Canadian high arctic permafrost[e]
Actinobacteria[f]			+		
Arthrobacter	+	+	+	+	+
Brachybacterium					+
Cellulomonas	+				
Frigoribacterium				+	
Kocuria		+			+
Micrococcus	+				+
Nocardiaceae (family)[g]				+	
Rhodococcus	+	+			+
Promicromonospora	+				
Subtercola		+			
Bacteriodetes[f]			+		
Flavobacterium					+
Hymenobacter			+	+	
Pedobacter					+
Firmicutes			+		
Bacillus	+				+
Paenibacillus					+
Sporosarcina		+			+
Staphylococcus					+
Proteobacteria[f]			+		
Aeromonas	+				
Aztobacter	+				
Brevundimonas				+	
Oxalobaceraceae (family)[g]				+	
Polaromonas		+			
Pseudomonas	+				+

[a] Gilichinsky et al. (2007), [b] Blanco et al. (2012), [c] Aislabie et al. (2006b), [d] Aislabie et al. (2006a), [e] Steven et al. (2007, 2008, 2009), [f] could not be classified past the phylum level, and [g] could not be classified past the family level

associated with these metabolisms have been detected in permafrost with a protein microarray (Blanco et al. 2012). Whether the detection of these enzymes is reflective of in situ metabolisms, or whether the stable and cold preservative properties of Antarctic permafrost are preserving these biomolecules, similarly remains to be elucidated.

Aerobic heterotrophic microorganisms are the most commonly cultured from Antarctic permafrost, but their potential metabolic activity in permafrost under in situ conditions is generally uncharacterized. In surface soils of the Dry Valleys, soil CO_2 efflux has been detected under summer ambient conditions, indicating microbial respiration may be occurring in situ (Burkins et al. 2001; Parsons et al. 2004). After taking isotopic C composition into account, Shanhun et al. (2012) concluded that the CO_2 soil fluxes observed in surface and subsurface Dry Valley soils are partially abiotic in origin and that previous measurements likely overestimated the in situ activity of heterotrophic microorganisms in Dry Valley soils (Shanhun et al. 2012). In Arctic permafrost, soil CO_2 flux has been detected in high Arctic permafrost during both summer and late-winter ambient conditions (Whyte et al. unpublished) and in permafrost microcosm experiments at temperatures low as −15 °C (Steven et al. 2008) to −25 °C (Mykytczuk et al. 2013).

11.3 Adaptation to Permafrost

Because the primary source of liquid water in subzero environments results from freezing-point depression caused by increased solute and salt concentrations, many of the microbial adaptations to subzero temperatures include mechanisms to cope with osmotic stress (Chin et al. 2010; Mykytczuk et al. 2013). As result, many of the culturable microorganisms isolated from cryoenvironments are observed to be halotolerant or halophiles. For example, *Planococcus halocryophilus* strain Or1, isolated from high Arctic permafrost active layer, can grow at −15 °C in 18 % NaCl and is metabolically active at −25 °C in frozen permafrost microcosms. This strain possesses a suite of adaptations to cope with osmolyte and cold stresses, such as multiple copies of osmolyte uptake genes, increased protein flexibility, and resource efficiency (Mykytczuk et al. 2011, 2013). Reviews on cold-adaptation mechanisms identified in microorganism have been discussed extensively elsewhere (Bakermans et al. 2009; Qiu et al. 2009). In addition, cold-adapted microorganisms can decrease energy metabolism, or go into a state of dormancy to resist cellular damage; these adaptations promote long-term survival in permanently cold environments (Bakermans et al. 2009; Casanueva et al. 2010). Cyst-like resting cells with thickened cell walls and capsular layers, as well as miniature cells 0.3 cm–0.5 μm in diameter, have also been observed in Antarctic permafrost samples. Such adaptations have been proposed to aid cryoprotection on long-term scales (Gilichinsky et al. 2007; Soina et al. 2004).

11.4 Ancient Life in the Subsurface

The Antarctic contains some of the Earth's oldest sediments and thus may represent the largest reservoir for ancient microbial life on the planet. Due to the preservative properties of permafrost and ice environments (i.e., stable and permanently cold temperatures), nucleic acids and biomolecules may be able to be maintained over long time-scales. Lower rates of decay, an order of magnitude for every 10 °C drop, should allow extraction of biomolecules from sediments as old as 1 million years (Willerslev et al. 2004). In spite of the constant cold temperatures, with increasing age, damage to nucleic acids will accumulate. Processes that can reduce the integrity of nucleic acids and biomolecules over time include ionizing background radiation, alkylation, hydrolytic and oxidative damage causing depurination, cross-linking, and single-stranded and double-stranded breaks of nucleic acids (Hansen et al. 2006; Amato et al. 2010). DNA preserved in Siberian Arctic permafrost ~100,000–400,000 years old was found to have an increased frequency of cross-linked DNA with age (Hansen et al. 2006). Cross-linking and single-stranded breaks inhibit PCR amplification or cause the generation of short PCR fragments, which may impede molecular surveys of microbiota. Metabolically active cells in permafrost could increase the longevity of their DNA with active DNA repair systems. Data on the metabolic rates associated with the survival of immobilized, starved, and possibly dormant microbes thought to exist in permafrost suggest that rates of repair of DNA and protein damage in living microbes are similar to rates of incurred damage (Price and Sowers 2004). Lastly, the successful isolation of ancient permafrost bacteria or intact genes or pathways through metagenome analyses, especially from the relatively very old Antarctic permafrost, may serve as novel sources of biomolecules for biotechnology (enzymes, compatible solutes) and health applications (novel antimicrobials) or, for example, elucidating the evolution of resistance mechanisms to antibiotics, as was recently done in high Arctic permafrost.

11.5 Astrobiology Implications of Antarctic Permafrost

Currently, the most promising planetary bodies in which we look for life are all extremely cold. Europa (a moon of Jupiter) and Enceladus (a moon of Saturn) are icy bodies where there is evidence for subsurface liquid water in spite of average surface temperatures of −160 and −190 °C, respectively (McKay et al. 2012). Mars possesses ample evidence of past liquid water, and the current presence of ice-rich ground beneath dry, extremely cold soils as observed by the Pheonix lander (Mellon et al. 2009). In addition, gullies formed on the sides of craters during the past decade on Mars provide compelling evidence that liquid water (or brine) may exist on Mars (Malin et al. 2006; McEwen et al. 2011), potentially derived from subzero saline springs in deep permafrost cryoenvironments like those that exist on Earth (Lay et al. 2012; Niederberger et al. 2010). Summer ground temperature maxima of 20 °C also make Mars a primary target of astrobiological investigations of past or present life (McKay et al. 2012). In this respect, Antarctic permafrost located in the higher-elevation MDVs are considered to be the most Mars-like due to their extreme aridity and cold temperatures, and because, they are the only place on Earth known to contain both dry permafrost overlaying ice-cemented permafrost. UV, a high-elevation MDV (1,700 m.a.sl.), has ambient air temperatures which never rise above freezing and contains ice-cemented ground underneath dry-permafrost surface soils at depths that range from a few centimeters to over 98 cm. In some parts of this valley, an active layer which rises above 0 °C (due to solar heating) is completely absent (Marinova et al. 2013).

As on Mars, the presence of perchlorates is found in the dry-permafrost soils (Kounaves et al. 2010; Hecht et al. 2009); Perchlorates are efficient freezing-point depressants (eutectic point −67 °C) and can also be used as an electron acceptor for anaerobic microbial respiration (Coates and Achenbach 2004). Microbial investigations of UV show detectable amounts of nucleic acids, phospholipids (Tamppari et al. 2012), and the presence of relatively low amounts of microorganisms based on microscopic cell counts (Table 11.1) (Goordial unpublished). However, sensitive radiorespiration assays completed on UV permafrost samples have yielded little to no measureable microbial activity at subzero temperatures (Goordial unpublished). More studies need to be carried out in upper Dry Valley permafrost and other similar cryoenvironments on Earth in order to determine how we can best search for and measure active and/or preserved microorganisms and biosignatures on other astrobiology targets.

11.6 Conclusion

Antarctica contains almost half of the world's permafrost and is host to some of the most extreme conditions on Earth. Permafrost in the Mars-like hyperarid soils of the upper Dry Valleys, or the permafrost underlying the Antarctic Ice sheet, are compelling cryoenvironments to examine the limits and longevity of life and biomolecules in cryoenvironments. Tantalizing results from the Arctic strongly indicate that metabolically active microbial ecosystems exist in Arctic permafrost (Steven 2008; Rivkina et al. 2000), as well as in the bedrock underneath kilometer-thick ice sheets (Miteva et al. 2004); However, whether similar active microbial ecosystems inhabit the more extreme Antarctic permafrost, especially in the harsh dry valley sites, remains to be determined. Are the microorganisms present in Antarctic permafrost viable and active in situ, or do they represent cryopreserved microfossils which have been frozen on geological timescales? How long can cells or biomolecules be preserved in the environment? How can we detect the expected extremely slow or minute microbial activity in such permafrost soils? These are important and fundamental questions that remain to be addressed, but which are crucial to our understanding of the ecology of Antarctic permafrost soils. Additionally, understanding the microbiology of permafrost will inform us in how to best search for and identify the presence and/or activities of similar microbial communities that could exist or have existed on other bodies in our solar system rich in permafrost features.

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Chapter 12
Primary Production and Links to Carbon Cycling in Antarctic Soils

D. W. Hopkins, K. K. Newsham and J. A. J. Dungait

Abstract Antarctica is not a single ecological model. Substantial differences in the temperature, precipitation (which combine to affect the available water) and radiation determine the distribution and the habit of primary producers that in turn structure the trophic. Because terrestrial primary production is operating at environmental extremes in some parts of Antarctica, particularly in continental Antarctica, the spatial and temporal subsidies to the terrestrial stock of organic carbon make proportionately larger contributions to contemporary carbon cycling.

12.1 Introduction

In this chapter, we provide an overview of the distribution of primary producers (Figs. 12.1 and 12.2) and the environmental controls on primary production in terrestrial Antarctica and assemble estimates of the rates of primary production in different biogeographic regions of Antarctica. Our emphases are on the differences in the environmental controls for different parts of the Antarctic and on the contribution that primary producers make to other ecosystem processes as the sources of energy and organic substrates for other organisms in terrestrial Antarctica. Primary production and associated carbon cycling in Antarctica differ markedly from other terrestrial ecosystems for the following reasons:

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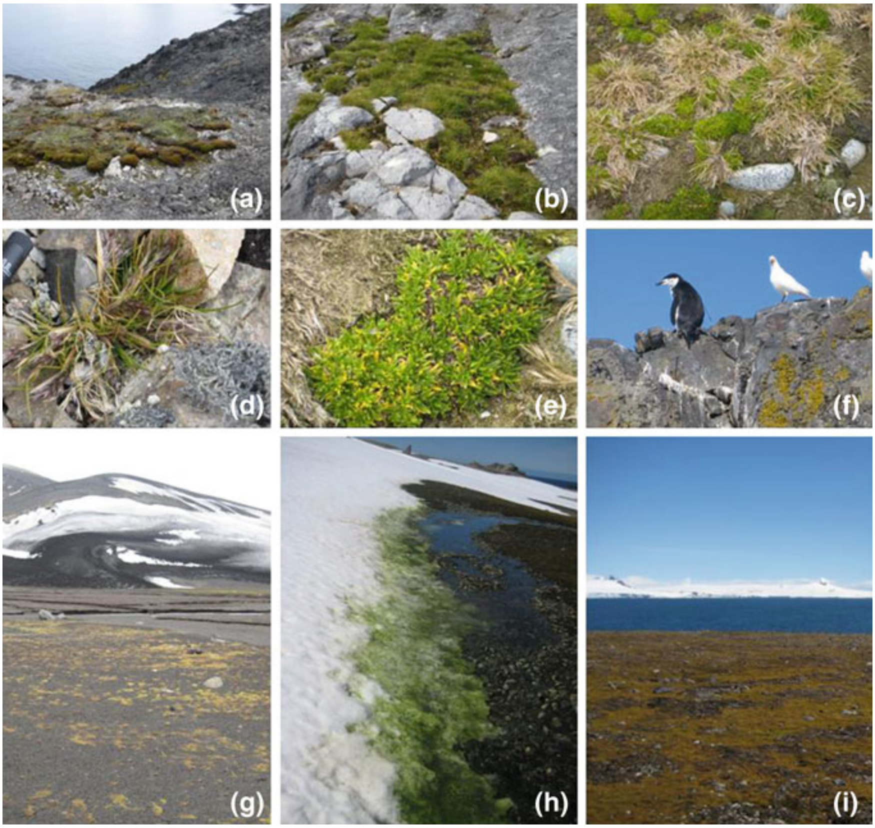


Fig. 12.1 Montage of photographs of different primary producers in the maritime Antarctic. **a** *Deschampsia antarctica* (grass) growing on a well-established shallow peat bed; **b** a lawn of *D. antarctica* on a cliff ledge; **c** *D. antarctica* and *Colobanthus quitensis* (dicotyledonous plant); **d** isolated *D. antarctica* in close proximity to a fructose lichen, *Cladonia* sp.; **e** a small *C. quitensis* colony; **f** *Xanthoria* sp. (lichen) on cliff face; **g** extensive *D. antarctica* on volcanic derived soil; **h** green snow algae; and **i** mixed moss and lichen lawn

1. Primary production in the ecosystems of Antarctica is only rarely dominated by higher plants. For large parts of the Antarctica where photosynthesis can occur, higher plants are absent and photoautotrophic and chemoautotrophic bacteria, eukaryotic algae, lichens, liverworts and mosses are significant contributors to carbon fixation depending on the location.
2. Many of the primary producers are cryptic organisms either because they are microscopic or because they live just below the soil or rock surface (hypolithically) or inside the rocks (endolithically), where they are protected from the more extreme environmental conditions.
3. In many parts of Antarctica, in situ contemporary primary production occurs at very low rates and in spatially isolated sites defined by the supply of resources such as water and where environmental conditions permit. Under these

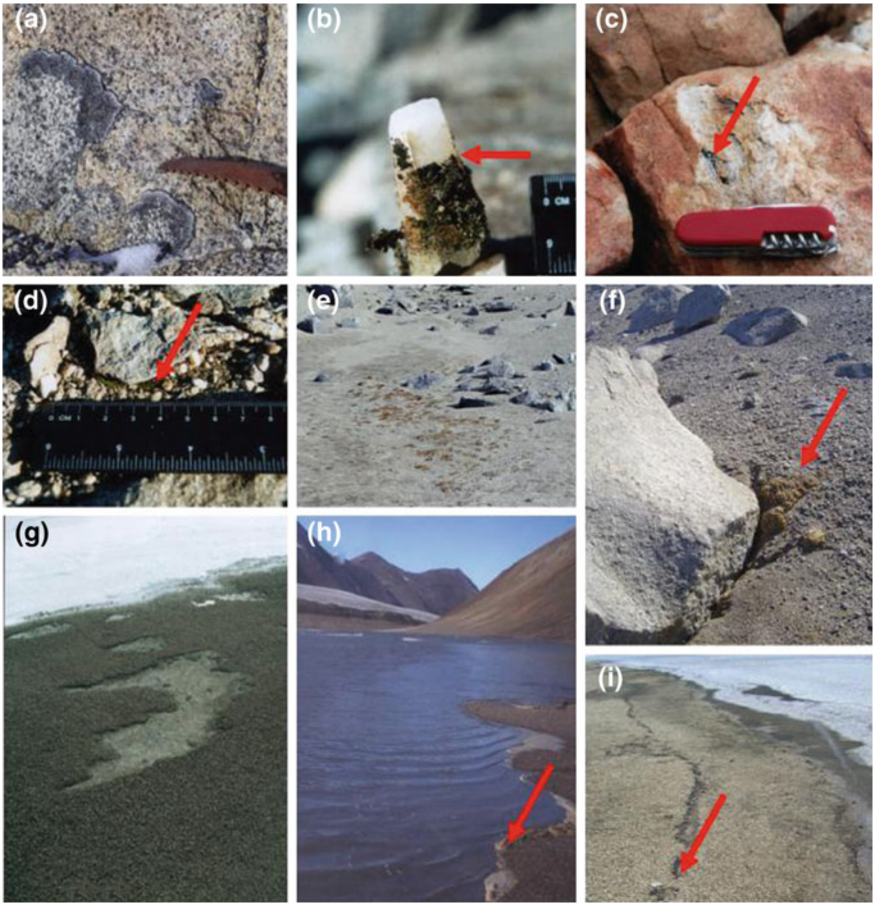


Fig. 12.2 Montage of photographs of different primary producers in the Dry Valleys, continental Antarctica. **a** *Buella frigida* (moss) growing on rock surface; **b** hypolithic algal-based community on a marble stone; **c** endolithic lichen-based community in sandstone; **d** *Bryum* sp. (moss) growing in the sheltered leeside of a stone; **e** moss colony of moss in an ephemeral stream bed; **f** dried organic deposit exposed at the soil surface presumed to be ancient lake deposit derived from algae and cyanobacteria; **g** algal and cyanobacteria mat at a lake margin; **h** algal- and cyanobacterial-derived foam at a lake margin; and **i** stranded algal and cyanobacteria detritus at a lake margin

circumstances, organic carbon fixed by photosynthesis in, for example, lakes and the oceans, and then transferred to the land surface (spatial subsidies), or as a result of recycling of palaeodeposits entering contemporary carbon cycling processes (temporal subsidies or "legacies") can make significant contributions to the organic carbon in the soils. Such subsidies almost certainly occur in all terrestrial ecosystems, but because the in situ, contemporary primary production is often so small in Antarctica, subsidies can make a larger proportional contribution to carbon cycling.

12.2 Biogeographic Zones

The extreme cold, and in some cases the combination of extreme cold and dryness, restricts the distribution and activity of primary producers, leading to a broad generalisation that primary production in Antarctica is low in comparison with other parts of the world. However, this belies the underlying diversity and it is therefore necessary to consider different biogeographic zones separately. There are sufficient differences in the ecosystems between the sub-Antarctic, the maritime Antarctic and continental Antarctica, which may be subdivided into the coastal regions of the continent and the inland deserts (e.g. the Dry Valleys) and isolated nunataks, for

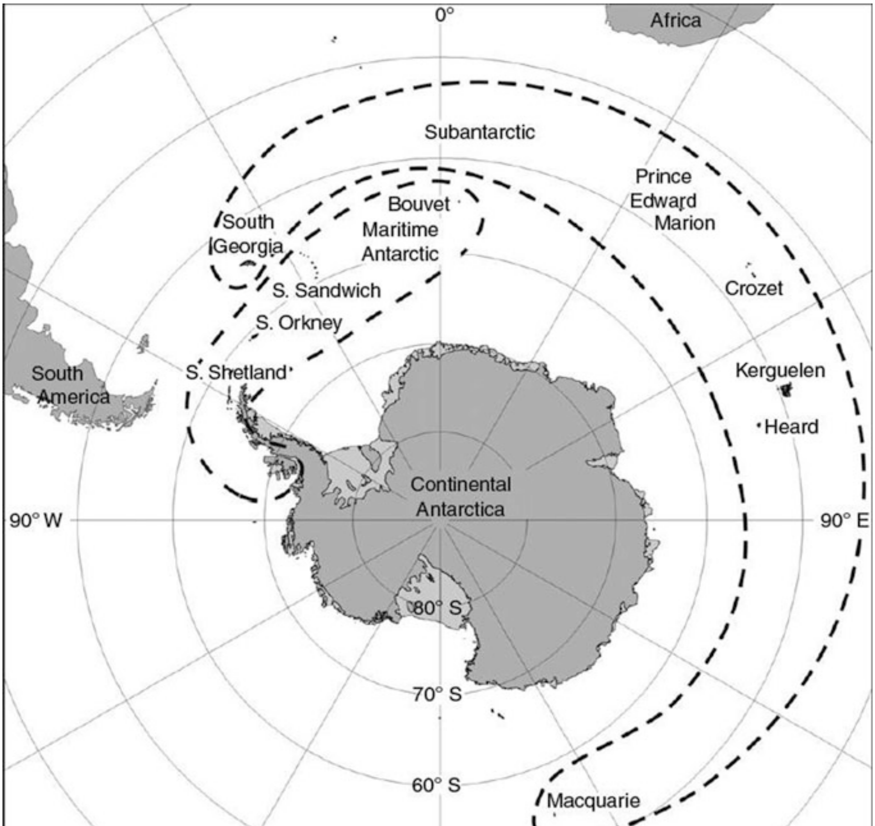


Fig. 12.3 Map of Antarctic showing the major biogeographic zones

Table 12.1 Summary of air temperature ranges for biogeographic zones of Antarctica. Adapted from Convey (2013)

Biogeographic zone	Months with mean air temperatures above 0 °C		Microhabitat temperature range (0 °C)			
	Maximum	Minimum	Summer		Winter	
			Maximum	Minimum	Maximum	Minimum
Sub-Antarctic	12	6	30	−5	−2	−10
Maritime Antarctic	4	1	30	−5	3	−40
Coastal continental Antarctica	1	0	30	−10	−10	−40
Inland continental Antarctica	0	0	20	−30	−50	−60

Table 12.2 Species richness of the plants in Antarctica adapted from Convey (2013) and estimates of contemporary, in situ primary production (see text for details and assumptions)

Biogeographic zone	Flowering plants	Ferns and allies	Mosses	Liverworts	Lichens
Sub-Antarctic	60	16	250	85	250
Maritime Antarctic	2	0	100	25	250
Continental Antarctica	0	0	25	1	150

these zones to provide a convenient approach for examining some of the diversity between primary producers (Fig. 12.3). Summary of temperature and the plant richness for these biogeographic zones is provided in Tables 12.1 and 12.2.

12.2.1 Sub-Antarctic

The sub-Antarctic includes the islands of South Georgia, Heard Island and McDonald Islands south of the Antarctic convergence and Marion Island, Macquarie Island, the Crozet archipelago and the Kerguelen archipelago which are closer to or north of the Antarctic convergence (Convey 2013). In some studies, islands further north, such as the Falkland Islands, at 52°S, are also included in Antarctic latitudinal transects, but in our opinion, this is stretching transects to artificial end-members. By Antarctic standards, the temperature regimes in the sub-Antarctic are relatively mild in part because of the strong maritime influence coupled with the relatively northerly location. The diversity of primary producers in the sub-Antarctica is the greatest of the four zones, and this is the zone where flowering plants are the most abundant (Table 12.2).

12.2.2 Maritime Antarctica

The maritime Antarctic includes the western coastal regions of the Antarctic Peninsula as far south as Alexander Island (72°S), the eastern coast of the peninsula to 63 °S, the Scotia Arc (the South Orkney, South Shetland and South Sandwich Islands) and the isolated Bouvetøya and Peter I Øya. The maritime influence leads to positive summer temperature maxima and short thaws during the winter, as well as generally high precipitation (Convey 2013). The zone also includes active volcanoes, which lead to localised geothermal heating, which leads to distinctive communities of primary producers. At the large scale, there is significant variation in the day length during the year, with increasing winter darkness further south (Fig. 12.4). This reduces the period when there is sufficient daylight for photosynthesis, but since the water is usually unavailable for a longer period due to sub-zero temperatures, day length *per se* is not likely to be the limiting factor for photosynthesis. During the summer, incident UVB radiation may constrain photosynthesis because of photoinhibition (Holm-Hansen et al. 1993) and many primary producers either have protective pigments to mitigate the potentially damaging effects of UV radiation or grow in protected habitats, thereby avoiding UV radiation (Wynn-Williams 1994).

The abundance of flowering plants generally declines to the south (Table 12.2), with increasing dominance of microbial and cryptogam primary producers. However, local and microhabitat conditions have led to isolated pockets of flowering plants as far south as latitude 69°S at the northern tip of Alexander Island, an observation that at the time substantially extended the southern limit of flowering plants, and which is unlikely to be range expansion associated with recent climate warming because the communities were very well developed and occurred on peat deposits of likely to be a century or more old (Convey et al. 2011). The distinctions between the biogeographic zones summarised here are based on environmental conditions, but there is an evolutionary disjunction between the southern Antarctic

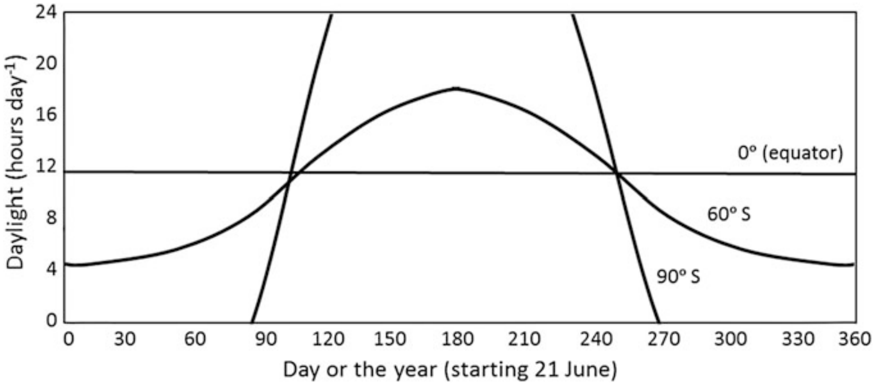


Fig. 12.4 Daylight regimes at different latitudes

Peninsula and West Antarctica, the Gressitt Line (Chown and Convey 2007), suggesting a phase of evolutionary isolation between the peninsula and West Antarctica.

12.2.3 Continental Antarctica

Most of the land area of Antarctica is taken up by the continent (both East and West Antarctica), but the vast majority of this area is not ice free at any time during the year. The Dry Valleys in Victoria Land are the largest contiguous or near-contiguous ice-free region and one of the most extreme terrestrial ecosystems on the Earth characterised by both low temperatures and low precipitation, much of which is ablated, leading to extreme dryness and the Dry Valleys being regarded as the largest expanse of polar desert. Other than the Dry Valleys, the remaining ice-free land is isolated nunataks and isolated stretches of coastline. Most of continental Antarctic falls within the Antarctic Circle and therefore experiences winter darkness, short summers, low solar angle and limited photosynthetically active radiation (Fig. 12.4). This extreme solar regime contributes to the low temperature regime (Table 12.1), but it also leads to seasonal periodicity that affects the temporal and spatial distribution of photosynthetically derived organic matter (Hopkins et al. 2006a).

12.3 Biochemistry of Primary Production

As with nearly all terrestrial ecosystems, primary production in Antarctica is predominantly driven by photosynthesis in which photoautotrophic organisms use radiation harnessed by chlorophyll as the energy source to drive the reduction of CO_2 into organic C. Where the photosynthetic organisms are inconspicuous and actual rates of photosynthesis are small (sometimes at the limit of detection), such as occurs in the polar deserts, soil chlorophyll concentration is often used as a proxy for primary production (Barrett et al. 2006). Using the chlorophyll concentration to infer photosynthesis is particularly relevant in the Dry Valleys where the environmental conditions and high carbonate concentrations can lead to net CO_2 flux into the soil (Parsons et al. 2004; Shanhun et al. 2012), confounding the interpretation of CO_2 influx as photosynthesis.

Chemoautotrophy, in which reducing power from oxidation reactions drives CO_2 reduction to organic carbon by chemoautotrophic bacteria (e.g. nitrifying bacteria), also contributes to primary production. In most terrestrial ecosystems, primary production from chemoautotrophy is a minor contributor to primary production. Where overall primary production is small it is possible that chemoautotrophs may make a relatively large contribution to primary production, but although nitrifying bacteria and nitrification have been detected in Antarctic soils (Wilson et al. 1997; Hopkins et al. 2006b; Chan et al. 2013), the magnitude of their contribution to carbon cycling is unknown.

12.4 In Situ Primary Production

The occurrence of significant net primary production depends on environmental conditions and the distribution of organisms. Figure 12.5 summarises relationships between some soil and climatic factors and primary producers along a transect from the polar plateau through the Transantarctic Mountains towards the coast. Within the Dry Valleys, primary producers adopt different habits, including the development of epilithic, hypolithic and endolithic communities, on hillslopes and desert pavements in dry habitats, and microbial mat and filamentous communities in wetter habitats, such as lake margins and in stream beds. Cyanobacteria often dominate the primary producer biomass, with, for example, *Nostoc commune* forming conspicuous films and mats in ephemeral streams and at lake margins during summer (Vincent 1988; Novis et al. 2007), as well as growing epiphytically on mosses (Alfinito et al. 1998), and with *Gloeocapsa* sp. adapted to extremely dry conditions by growing endolithically (Friedmann and Ocampo 1976; Friedmann 1982; Friedmann et al. 1993). Eukaryotic algae are widely reported in Antarctica from most ice-free areas, including in ephemeral streams and at lake margins, on

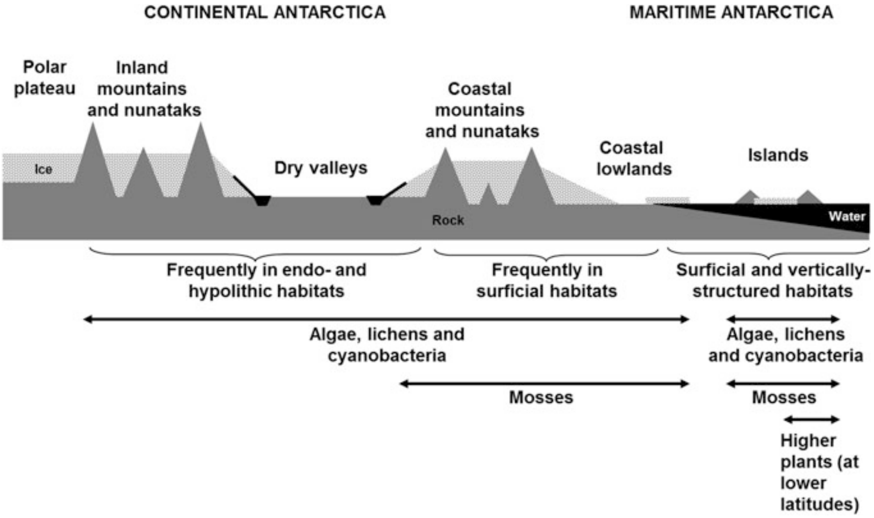


Fig. 12.5 Generalized relations of ice and liquid water distribution, net water fluxes, prevailing winds and primary producers with geomorphology in Antarctica. The diagram has been adapted from Janetschek (1970) and Hopkins et al. (2006a)

wetter soils, as epiphytes on mosses, in cyanobacterial mats and predominantly in lakes (Cathey et al. 1981; Hawes and Schwarz 1999; Pocock et al. 2004). Mosses form conspicuous communities even in the extreme conditions of the dry valleys, where they are associated with wet seeps and springs, and less obviously beneath a thin layer of translucent soil particles and on the soil surface fringing stones sheltered from the wind, but their abundance is far greater in the maritime Antarctic and sub-Antarctic. Under the less extreme environmental conditions experienced in the maritime Antarctic, with greater biological diversity and abundance, the primary producers are less sparse and mosses, liverworts and flowering plants become more conspicuous. Although they are distributed according to suitable environmental conditions—chiefly the availability of liquid water during the summer months—the less extreme environment leads to more contiguous cover and greater biomass, with, for example, continuous patches of mosses and higher plants in the Léonie Islands in Ryder Bay (67°S) reaching >10 m^2 in area (Fretwell et al. 2011). Continuous stands of mosses attain greater areas (up to *c.* 530 m^2) on the Argentine Islands at 65°S (Smith and Corner 1973), whereas, at Signy Island in the South Orkney Islands (60°S), although stands of plant species on the island are often as little as 15 m^2 in area, individual stands of *Chorisodontium aciphyllum* can reach >900 m^2 in area (Smith 1972).

There are estimates of net primary production for selected organisms and for the biomass of some groups of primary producers at selected sites in the continental Antarctica (Green et al. 1998; Kappen et al. 1998; Schwarz et al. 1992; Pannewitz et al. 2005, 2006). However, these data are sparse on a unit area basis and over a range of environmental conditions; thus, estimating net primary production is difficult. Friedmann et al. (1993) estimated the net primary production between 11 and 17 kg C ha^{-1} $year^{-1}$ for the endolithic microbial community in the Dry Valleys, of which 50–85 g C ha^{-1} $year^{-1}$ enters microbial biomass and the remaining metabolites percolate into soils and rocks and are potentially available to heterotrophs. However, they stress that this production may be restricted to as little as 20 % of the surface area in the Dry Valleys. It is generally assumed that the growth rate of primary producers in the Dry Valleys is slow (Johnston and Vestal 1991), with Bonani et al. (1988) making a preliminary report that crypotendolithic organisms from the Dry Valleys may be thousands of years old. Ephemeral water flow, which may represent only a few percentage of the land surface (Elberling et al. 2006), is a significant hot spot of productivity capable of rapid responses to incoming water (Conovitz et al. 2006; McKnight et al. 1999). For comparison, Noy-Meir (1973) estimated above- and belowground productivity in excess of 1 t C ha^{-1} $year^{-1}$ for a range of hot desert ecosystems worldwide and up to ten times as much for semi-desert ecosystems.

The productivity of mosses, the main primary producers in many maritime Antarctic ecosystems, is well documented, with most values being derived from study sites on Signy Island (60 °S). Most of the values are expressed in g dry matter m^{-2} $year^{-1}$. In order to make comparison of primary productivity with the values for the Dry Valley above, we have assumed that the dry matter contains approximately 50 % C. In pure stands of the mosses, *Chorisodontium aciphyllum*, *Polytrichum strictum*, *Sanionia uncinata*, *Warnstorfia sarmentosa* and *Warnstorfia fontinaliopsis* on Signy Island have been estimated at 275–726 g dry mass m^{-2} $year^{-1}$, respectively (Longton 1970; Baker 1972; Collins 1973; Fenton 1978). This corresponds to between approximately 1,300 and 3,600 kg C ha^{-1} $year^{-1}$. The productivity of these species declines to 96–279 g dry mass m^{-2} $year^{-1}$ (approximately 480–1,400 kg C ha^{-1} $year^{-1}$) when growing in competition with other species (Davis 1981). Net primary production across all moss species on the two sites was estimated at approximately 400 g dry mass m^{-2} $year^{-1}$(approximately 2,000 kg C ha^{-1} $year^{-1}$), and that of the alga *Prasiola crispa* has been estimated at less than 20 g dry mass m^{-2} $year^{-1}$ (approximately 100 kg C ha^{-1} $year^{-1}$; Davis 1981). Further south at the Argentine Islands (65 °S), the annual net productivity of *Prasiloa alpestre* declines to about 400 g dry mass m^{-2} $year^{-1}$ (approximately 2,000 kg C ha^{-1} $year^{-1}$; Longton 1970).

Annual primary production at South Georgia in the sub-Antarctic (54°S) is typically much higher than in the maritime Antarctic. The annual productivity of *P. alpestre* is 450–500 g dry mass m^{-2} $year^{-1}$ (approximately 2,250–2,500 kg C ha^{-1} $year^{-1}$) on the island, whereas that of another moss, *Pohlia wahlenbergii*, is estimated at approximately 1,000 g m^{-2} $year^{-1}$ (approximately 5,000 kg C ha^{-1} $year^{-1}$) in mixed stands (Smith and Walton 1975). Of the higher plants at South Georgia, the annual productivity of *Festuca contracta* attains 160 g m^{-2} $year^{-1}$ (800 kg C ha^{-1} $year^{-1}$) in mixed stands, that of *Acaena magellanica* reaches 850 g m^{-2} $year^{-1}$ (4,250 kg C ha^{-1} $year^{-1}$) aboveground and 500 g m^{-2} $year^{-1}$ (2,500 kg C ha^{-1} $year^{-1}$) belowground, and that of tussock grass (*Paradiochloa flabellata*), which forms dense stands of >2 m in height in coastal areas, attains 5,000 and 1,000 g m^{-2} $year^{-1}$ (25,000 and 5,000 kg C ha^{-1} $year^{-1}$) aboveground and belowground, respectively (Smith and Walton 1975). Even the lichen *Cladonia rangiferina* attains a net productivity of approximately 100 g m^{-2} over 100 days at South Georgia (Smith and Walton 1975).

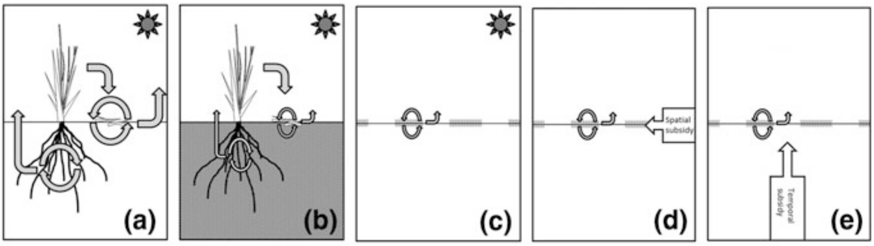
Although the data are fragmentary, from these preceding estimates, there is a trend of primary production declining with increasing latitude and with the transition from the maritime to continental Antarctica. Clearly, more work is required to collect and assemble sufficient estimates of primary production to be able to make ecosystem-level assessments of terrestrial primary production in Antarctica.

12.5 Temporal Subsidies

Considerable reference has been made to the role of ancient lake sediments as sources of soil organic matter in the Dry Valleys which has been redistributed by geomorphic processes (the so-called legacy C; Burkins et al. 2000). The evidence comprises C and N stable isotope signatures, which distinguish ancient C from contemporary sources, and indirect geomorphic evidence (Burkins et al. 2000). Large lakes with levels far higher than present may also have occurred in both the Wright Valley and Victoria Valley (Hall et al. 2001; Hall and Denton 2002), the sediments from which may also contribute to contemporary C cycling. Indeed, there are conspicuous deposits of algal detritus on lake terraces above Lake Vanda, the current lake in the Wright Valley (Hall et al. 2001), but their quantitative contribution to contemporary C cycling has not been investigated, and there are apparently no radiocarbon dates for soil organic matter. Estimates of the turnover of contemporary organic C in other Dry Valleys soils are fast, ranging between 20 and 120 years (Burkins et al. 2002; Elberling et al. 2006) supported by rapid mineralisation of soil C and N in laboratory studies (Barrett et al. 2002, 2004; Hopkins et al. 2006b). The implications of these fast turnover times are either that legacy C deposits may be about to be exhausted, or that the legacy C is either so stable or protected that it contributes little to contemporary C cycling. If the latter is true, contemporary C cycling in Dry Valleys soils must be sustained largely, if not exclusively, by modern sources of organic matter.

12.6 Spatial Subsidies

The relatively large standing biomass in lakes, most notably as cyanobacteria mats, and imbalances between primary production and consumption in the absence of macroconsumers make lakes obvious sources of organic resources (Elberling et al. 2006). Productivity in lakes in Dry Valleys is in the range 10–100 g C m^{-2} $year^{-1}$ (Vincent 1988). Transfer of only a modest fraction of this to the land surface could be sufficient to sustain the measured rates of soil respiration (Moorhead et al. 2003; Elberling et al. 2006). Rapid turnover of organic matter in dry valley soils is also consistent with regular inputs of relatively labile organic residues (Hopkins et al. 2006b; Elberling et al. 2006). Aeolian transport of lacustrine microbial mats, endolithic communities and organisms (Parker et al. 1982; Nienow and Friedmann 1993; Moorhead et al. 2003; Nkem et al. 2006; Wilson 1965) supports the hypothesis that particulate (modern) matter is transported from productive (lakes) to low-productivity sites (soils). Increases in soil respiration along transects towards a lake and the decreasing organic C concentration with soil depth provide indirect evidence of redistribution of lacustrine detritus from wet sites at lake edges to surrounding drier soils (Elberling et al. 2006; Hopkins et al. 2006b). This mechanism relies on lacustrine organic detritus washing up at the lake edge, where it is dried and dispersed by the wind (Fig. 12.6). Seasonal, diurnal and/or weather-dependent fluctuations in lake level resulting from periods when feeder streams stop flowing and glacier surfaces freeze may all contribute to wash-up and stranding of lacustrine detritus.



Carbon cycling linked to primary production by flowering plants with significant above and below-ground linkages. In this scenario, carbon inputs from primary production and decomposition are balanced so there is not net change in ecosystem carbon content.

Carbon cycling linked to primary production by flowering plants as with A (left). In this scenario, carbon inputs from primary production and decomposition are balanced so there is not net change in ecosystem carbon content.

Carbon cycling linked to primary production by surface living or endolithic or hypolithic primary producers (e.g. mosses, lichens, liverworts, algae and cyanobacteria). The major processes occur at or close to the soil or rock surface.

Carbon cycling linked to a spatial subsidy of primary production from other sites, such marine and lacustrine sites. The major processes occur at or close to the soil or rock surface.

Carbon cycling linked to a temporal subsidy of primary production that occurred in the past (i.e. a legacy) and which enters contemporary carbon cycling as deposits are exposed by geomorphic processes.

Fig. 12.6 *Above* and *belowground* linkages and the distribution of organic resources in the different Antarctic ecosystems (based on Wall 2012)

12.7 Aboveground–Belowground Linkages

The diversity of primary producers in the different regions of Antarctica determines the linkages between primary production and other carbon cycling processes. This is summarised in Fig. 12.6 derived from (Wall 2012), indicating the differences in vertical structuring and contrast between aboveground and belowground linkages.

Where higher plants are more abundant, such as in the maritime Antarctic and sub-Antarctic, there will typically be a root-associated community, which utilises carbon from the roots and contributes to other biogeochemical processes, and a litter-associated decomposer community, which is responsible primarily for the decomposition of plant detritus. The diversity and composition of these communities vary depending on site and environmental factors, but they will include heterotrophic bacteria and fungi, and invertebrates. In some cases, symbionts are also known to be present, with sparse colonisation by arbuscular mycorrhizal fungi in the roots of the two Antarctic higher plant species to as far south as the South Shetland Islands, and consistent colonisation of roots throughout the maritime Antarctic by dark septate endophytic fungi, which can enhance plant growth, possibly by mineralising peptides and amino acids in the rhizosphere (Upson et al. 2008, 2009).

Depending on the balance between primary production and decomposition, sites of organic matter accumulation and even peat accumulation may arise if primary production exceeds decomposition (Convey et al. 2011). The potential for decomposition is primarily a function of the biochemistry of plant litter. Lignin is assumed to confer recalcitrance on plant litter derived from vascular plants relative to non-lignified mosses and lichens. However, the emerging use of biochemical proxies for palaeoclimate change in peat bogs in the Northern Hemisphere ranging from wet temperate to tundra has suggested that moss detritus which is largely non-phenolic is more resistant to decomposition than that of vascular plants (Moore et al. 2007; Philben et al. in press). The resistance to decomposition is likely conferred by specific cell wall polysaccharides which, furthermore, may depress local decomposition (Hajek et al. 2011).

Where the principal producers are lichens, algae and cyanobacteria living endolithically or hypolithically, and even some mosses and lichens on the soil and rock surfaces, such as in continental Antarctica, the primary production occurs at spatially isolated sites (Wall 2012). There is rarely contiguous cover of primary producers, and there is little vertical penetration with the primary producers being concentrated at sites where resources and environmental conditions permit (Fig. 12.6). This means that the associated carbon cycling processes also occur in spatial isolated sites. By comparison with other terrestrial ecosystems, including some in Antarctica, physical processes such as meltwater flows and wind have a greater role in the redistribution of organic carbon.

Spatial isolation of primary producers, discontinuity in the presence of primary producers and physical factors that redistribute organic resources (i.e. that drive spatial and temporal subsidies) can determine the provenance of organic matter between different groups of primary producers. Following the work of Burkins et al. (2000) in the Taylor Dry Valley, Hopkins et al. (2009) used the ^{13}C and ^{15}N stable isotope composition of soil organic matter to show that lacustrine algae and cyanobacteria, possibly including ancient lake sediments, were the dominant source or organic matter in a small, sheltered valley with a relatively large amount of liquid water, whereas in larger more exposed and colder valleys with less liquid water (the Taylor, Wright and Victoria Valleys), lichens and mosses were the main contributors to the soil organic matter. Differences in the primary producer sources of the soil organic matter have potential implications for the carbon and other nutrient cycling processes in the soils, but this has not been explored. Assigning sources of organic inputs to specific groups of organisms using compound-specific stable isotope and radiocarbon analyses of established or novel biomarker molecules has the potential to increase the fundamental understanding of organic matter dynamics in Antarctic ecosystems and will complement the major new insights being provided to functional ecology by the application of modern molecular biological techniques.

12.8 Conclusions

It is important not to consider a single ecological model for Antarctica. Although the area where primary production is small, the size and biogeographic diversity of Antarctica to harbour several different trophic structures driven in part at least by primary producers. Substantial differences in the temperature, precipitation (which combine to affect the available water) and radiation determine the distribution and the habit of primary producers that in turn structure the trophic. Because terrestrial primary production is operating at environmental extremes in some parts of Antarctica, particularly in continental Antarctica, the spatial and temporal subsidies to the terrestrial stock of organic carbon make proportionately larger contributions to contemporary carbon cycling.

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Chapter 13
Climate Change and Microbial Populations

Etienne Yergeau

Abstract By 2100, the mean air temperature at the Earth's surface is predicted to increase by 1.4 °C to 5.8 °C, with a disproportionate effect at high altitudes and latitudes. This chapter reviews the currently available information regarding the responses of key microbial parameters, including diversity, community composition, abundance and functions, to climate change in Antarctic soils. For microorganisms inhabiting Antarctic soils, some insight has been gained by comparing microbial communities across latitudinal gradients, or through short-term laboratory incubations and field studies. Rapid responses of mosses, nematodes, soil algae, cyanobacteria, fungi, and bacteria have been observed in some Antarctic soils. Despite these interesting findings, it is difficult to specifically predict the effects of warming on Antarctic soil microorganisms. One reason is the extreme heterogeneity of soil habitats in this region, as they vary from moist eutrophic ornithogenic soils to nutrient- and water-limited Dry Valley soils. Climate change might have rapid and direct effects on soil microbes that are not otherwise limited, but the release of other limitations (e.g., water, nutrients) could be more important in several environments.

13.1 Introduction

Antarctic environments are extraordinary in the harshness of their climates, which are far more severe than northern climates at similar latitudes (Convey 2001). Environmental conditions are considered unfavourable in terrestrial Antarctic environments, with low thermal capacity of the substratum, frequent freeze–thaw and wet–dry cycles, low and transient precipitation, reduced humidity, rapid

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drainage and limited organic nutrients (Wynn-Williams 1990; Convey 1996). Furthermore, only 0.33 % of the Antarctic continent is ice free for some or all of the year (Fox et al. 1994), with much of this area representing cold rock deserts and nunataks. The vegetation of these ice-free habitats is characterized by low coverage and low productivity, being mainly composed of mosses and lichens, with only two vascular plant species. Antarctic food webs are consequently relatively simple and are characterized by the absence of insect and mammalian herbivores, so that most of the energy and materials found within primary producers enter a detritus, rather than a grazing, trophic pathway (Davis 1981; Heal and Block 1987). According to Kennedy (1996), cold temperatures and low moisture availability are probably the main limiting factors, resulting in the depauperate status of Antarctic habitats. Although the Antarctic continent has been isolated from other land masses for over 25 million years by the strong geophysical barriers of the Southern Ocean and South Polar Air Vortex, there is evidence that viable propagules can be transported from South America and around Antarctica (Marshall 1996; Hughes et al. 2004). Thus, aerobiological isolation probably does not limit microbial colonization. Biotic interactions such as predation and competition are also thought to play only a minor role in limiting life (Kennedy 1995; Convey 1996; Wall and Virginia 1999). Consequently, any amelioration in ambient temperatures, water availability or nutrient availability is expected to encourage the development of trophic complexity in these habitats (Kennedy 1995).

By 2100, the mean air temperature at the Earth's surface is predicted to increase by 1.4–5.8 °C, with a disproportionate effect at high altitudes and latitudes (Solomon et al. 2007). Strong regional differences are expected, especially in Antarctica. Indeed, a net cooling of Eastern Antarctica between 1966 and 2000 (Doran et al. 2002) appears to have coincided with a dramatic warming of the Antarctic Peninsula between 1951 and 2000, with an increase of 0.56 °C per decade (Turner et al. 2002), which resulted in the Antarctic Peninsula warming more rapidly than most other regions on the planet (Steig et al. 2009). Temperature increases in ice-free areas are expected to increase the availability of liquid water (originating from glacial and permafrost melting), potentially resulting in remarkable changes in ecosystem development (Cowan and Tow 2004). For instance, warming trends have been coupled to expanding ranges for vascular plants across the Antarctic Peninsula (Fowbert and Smith 1994; Smith 1994; Frenot et al. 2005; Convey and Smith 2006). For microbes, it was hypothesized that the responses of Antarctic soils will be driven mainly by nutrient and/or water limitations (Wynn-Williams 1996; Treonis et al. 2002; Wasley et al. 2006), similar to what is observed in Arctic soils (Ruess et al. 1999; Rinnan et al. 2007). In contrast, experimental evidence from a range of environments (including arctic and alpine systems) has suggested a variety of direct effects of warming on soil microbial communities (Zogg et al. 1997; Ruess et al. 1999; Deslippe et al. 2005; Rinnan et al. 2007) or associated nutrient cycling processes (de Klein and van Logtestijn 1996; Maag and Vinther 1996; Castaldi 2000; Dobbie and Smith 2001; Barnard et al. 2005). For microorganisms inhabiting Antarctic soils, some insight has been gained by comparing microbial communities across an Antarctic latitudinal gradient, which has been used as a proxy for predicting long-term climatic trends (Yergeau et al. 2007a, b, c, 2009), or through short-term laboratory incubations (Treonis et al. 2002; Bokhorst et al. 2007a; Newsham and Garstecki 2007; Yergeau and Kowalchuk 2008). The few field studies that have been reported to date have shown modest effects of warming on soil organic matter decomposition, as well as other soil processes and bacterial temperature sensitivity (Treonis et al. 2002; Bokhorst et al. 2007a; Rinnan et al. 2009). Rapid responses of mosses, nematodes, soil algae, cyanobacteria, fungi and bacteria have been observed in some Antarctic soils (Kennedy 1996; Wynn-Williams 1996; Convey and Wynn-Williams 2002; Dennis et al. 2012; Yergeau et al. 2012).

This book chapter reviews the relatively sparse information that is currently available regarding the responses of key microbial parameters, including diversity, community composition, abundance and functions, to climate change in Antarctic soils. Given the central role of microorganisms in Antarctic soil nutrient cycling, this knowledge is crucial for predicting the trajectory of Antarctic terrestrial environments in response to climate change. Antarctic terrestrial ecosystems represent excellent model systems for studying the effects of global warming on microorganisms: the relative simplicity of these environments facilitates the examination of microbial communities and activities without the confounding complexity of higher trophic levels (Smith 1996; Convey and Smith 2006). In the extreme Antarctic environment, small increments in temperature, nutrient or water availability have potentially greater biological impacts than changes on a similar scale in less extreme environments, simply because they represent relatively larger improvements to environmental conditions.

Climate change could affect Antarctic soil microorganisms in two ways: (1) directly, by increasing average temperature, decreasing the frequency of freeze–thaw cycles and increasing water availability and (2) indirectly, through changes in vegetation and soil nutrient cycling. Both direct and indirect effects of global warming could be different in the short term and in the long term. Integrating experimental and gradient studies may help to distinguish between the transient short-term effects of climate change and lasting longer-term effects (Kennedy 1996; Dunne et al. 2004).

13.2 Direct Influence on Microbes

13.2.1 Temperature

Bacterial processes are particularly sensitive to environmental conditions (Eriksson et al. 2001), yet bacteria are also highly adaptable to extreme and changing environments (Cavicchioli et al. 2000; Georlette et al. 2004; Thomas 2005). Many terrestrial Antarctic bacteria are believed to be cold tolerant as opposed to cold adapted (Line 1988; Wery et al. 2003; Aislabie et al. 2006). This may not be surprising as cold-tolerant organisms are better suited to survive the large and frequent variation in temperatures occurring in Antarctica than true cold-adapted microorganisms (Cowan and Tow 2004). This also implies that the selection pressure for low optimal growth temperature is relatively low compared with other environmental constraints (Vincent 2000).

Microbial responses to temperature are typically nonlinear, and therefore, it has been suggested that changes in temperature and climatic variability may have disproportionate effects on microbial communities and the functions for which they are responsible (Scherm and van Bruggen 1994). Most climate change scenarios predict not only a general warming trend, but also an increased variability in weather conditions (Solomon et al. 2007). This includes alterations in precipitation and thawing patterns, which will lead to more variable soil conditions (Groffman et al. 2001). Thus, predicted changes in temperature variability may have more profound consequences than increases in average temperature for Antarctic soil microorganisms, given the greater stress imposed by frequent temperature fluctuations as compared to gradual changes in average temperature (Vishniac 1993).

In the Antarctic, freeze–thaw cycles (FTC) are a common feature, and changes in the frequency of such events could have substantial effects on soil microbial communities and associated nutrient cycling functions. The freezing and thawing of soil has been shown to damage or destroy some microbial cells, releasing nutrients that become available to surviving microbes, which then become highly active during periods of thaw (Skogland et al. 1988; Christensen and Tiedje 1990). Extra substrate and nutrients can also be released from the physical disruption of soil aggregates due to frost action (Christensen and Christensen 1991; Edwards and Cresser 1992), resulting in altered microniches (Skogland et al. 1988). The penetration and effect of freezing and subsequent thawing depend on the level of insulation provided by vegetation and snow cover (Edwards and Cresser 1992). FTCs are also believed to play an important role in nutrient cycling in the Antarctic because they induce changes in exudation patterns of cryptogams (members of a formerly recognized taxonomic group that included all seedless plants and plantlike organisms) (Tearle 1987; Melick and Seppelt 1992; Melick et al. 1994). It has been estimated that freeze–thaw events induce an annual release of >15 % of the total organic matter of Antarctic cryptogams to the soil microbiota (Tearle 1987), an input that is ten times greater than what is estimated to arise from the decomposition of dead subsurface vegetation materials (Davis 1986). Accordingly, the frequency of FTCs was identified as a potentially important driving factor for the structuring of microbes involved in the C-cycle in Antarctic soils (Yergeau et al. 2007b).

13.2.2 Water

Water is a major limiting factor in some Antarctic environments, and changes in climate might partly relieve this limitation. Water limitation generally increases with increasing latitude (Kennedy 1993). Climate change could help relieve water limitations at some sites by (1) increasing precipitation, (2) changing precipitation patterns, with rain replacing snow, (3) increasing water availability through increased glacier and permafrost melting and (4) increasing the period of time when water is available (longer growing season).

13.3 Indirect Influence on Microbes

As mentioned above, most of the microorganisms in Antarctic soils are believed to be cold tolerant as opposed to cold adapted. Consequently, it has been hypothesized that the direct effects of increasing temperature on Antarctic soilborne microorganisms will be less important than indirect effects, such as changes in vegetation density and other associated soil biophysical properties (Vishniac 1993; Panikov 1999).

13.3.1 Plants

It has been suggested that ongoing climatic changes are steering existing terrestrial communities of the maritime Antarctic towards a more Magellanic or Patagonian composition (Kennedy 1996). The rapid warming rate of this region (2.8 °C since 1950, Turner et al. 2002) combined with the presence of a propagule bank in soils (Kennedy 1996) might speed up this shift in community composition. In fact, regional warming in the past decades has already led to a massive increase in the distribution of native Antarctic vascular plants (Fowbert and Smith 1994) and, together with an increased human presence, has also led to the introduction of non-native vascular plants (Molina-Montenegro et al. 2012). A recent study suggested that one of the two native Antarctic vascular plants, *Deschampsia antarctica,* has the ability to successfully compete with both soil microbes and moss for proteinaceous N at an early stage of decomposition that could explain the increasing success of this vascular plant as the maritime Antarctic warms (Hill et al. 2011). In ice-free areas that are too cold to support significant plant growth, indirect effects of climate change could also be seen through shifts in other primary producers such as lichens and cyanobacteria.

In the absence of consumers from higher trophic levels, such as herbivores, the link between plant and microbes is thought to be more important in Antarctic soils than in other environments, since a larger portion of the plant remains is made available to microorganisms. In fact, Antarctic soil microbial communities are significantly different between sparsely and densely vegetated environments (Yergeau et al. 2007a, 2009, 2012) and between rhizosphere and bulk soil of vascular plants (Teixeira et al. 2013). Not only is plant presence an important factor in structuring microbial communities, but also plant identity is of major importance, as different plant species exude distinct organic compounds, selecting for unique microbial communities (Kowalchuk et al. 2010). Roberts and colleagues (2009) recorded higher concentrations of nitrate, total dissolved nitrogen, DOC, DON and free amino acids in soil under *D. antarctica* and *Colobanthus quitensis* than in lichen- or moss-dominated soils. As the majority of Antarctic plants are low rising and densely cover the ground below them, the presence of plants also provides a sort of physical sheltering to soil microbes. This physical sheltering means that water and temperature conditions are less variable under dense plant cover when compared with environments lacking this cover.

13.3.2 Birds

Climate warming and associated sea ice reduction in Antarctica have modified habitat conditions for certain Antarctic bird species including penguins, and these birds now demonstrate remarkable population responses to regional warming (Forcada et al. 2006). In the maritime Antarctic, densely vegetated sites covered by lichens, mosses and vascular plants are often linked to bird activity (Simas et al. 2008) and these soils are hot spots of microbial activity. Organic matter rich in carbon, nitrogen and phosphorus is added to the soil in the form of guano, feathers, eggshells and bird remains, which leads to the formation of ornithogenic soils (Aislabie et al. 2009) (Chap. 6). These soils can occur at active or abandoned penguin colonies, but also nearby rookeries of other large birds (e.g. skuas, petrels). Not only do birds change soil conditions for microbial life, but they also continuously inoculate soil with microorganisms through guano deposition. Recent work has indicated that the effect of birds on soil microbial communities varies with the extent and the type of ornithogenic input and, in highly ornithogenic soils, seems to be modulated by the species of bird present, due to differences in diet (Teixeira et al. 2013). The authors hypothesized that climate change will not only directly influence Antarctic soil microbial communities, but also indirectly influence them through shifts in bird populations (Teixeira et al. 2013).

13.3.3 Other Soil Organisms

Other soil organisms may also influence microbes in their response to climate change. For instance, some soil fauna (e.g. nematodes, protozoa) prey on bacteria and shifts in the populations of these species following climate change will influence bacterial populations. Antarctic nematodes have been shown to prefer certain microbial prey species (Newsham et al. 2004), which could induce indirect shifts in microbial community composition following climate change.

13.4 Observed Microbial Shifts

This section focuses on the shifts observed in microbial communities following experimental climate change in the field or in the laboratory. The variability between habitats and even within habitats makes it particularly difficult to generalize any of the trends observed.

13.4.1 Field Experimental Manipulation

The logistics of establishing and maintaining long-term field experiments in the Antarctic are very challenging, and up to now, very few studies were conducted. In one instance, microbial crusts consisting predominantly of filamentous cyanobacteria covered 74 % of the soil after 3 years of warming compared to only 5 % coverage for controls (Wynn-Williams 1993). However, comparison of colonization between different sites showed that water limitations may outweigh the effects of temperature (Wynn-Williams 1996). Wynn-Williams (1996) also reported that the nature and extent of warming responses in frost-sorted polygon soils depended on the composition of the initial microflora. For instance, N_2-fixing cyanobacteria had a selective advantage specifically in N-limited fell-field (Wynn-Williams 1996).

Another study established warmed plots using open-top chambers (OTCs) at three different locations spread across 1,900 km in the Antarctic and sub-Antarctic. At each of these locations, densely vegetated and scarcely vegetated plots were established. Following two years of manipulation, very limited effects were observed on vegetation, arthropods, soil respiration and decomposition (Bokhorst et al. 2007a, b, 2008). Decomposition was more strongly influenced by local substratum characteristics (especially soil N availability) and plant functional type composition than by large-scale temperature differences (Bokhorst et al. 2007a). However, after three years of manipulation, differences did emerge, with an average of 33 % higher soil respiration in warmed plots (Yergeau et al. 2012). This increase in respiration was linked to a consistent increase in the abundance of fungi across all plots and an increase in bacterial abundance in densely vegetated plots (Yergeau et al. 2012). Consistent shifts across all environments were also observed in bacterial community composition, with a decrease in *Acidobacteria* and an increase in *Alphaproteobacteria* with warming (Yergeau et al. 2012). These shifts could also be linked to increased respiration as *Acidobacteria* generally display an oligotrophic lifestyle (slow growers) and *Alphaproteobacteria* are generally thought of as copiotrophs (fast growers) (Yergeau et al. 2012). Following warming, there was also a decrease in the functional redundancy of microorganisms, with fewer variants of several key functional genes being detected (Yergeau et al. 2012). All these results suggest increased nutrient availability following warming, but this trend remains to be confirmed over longer time scales. In contrast, three years of warming did not significantly alter bacterial temperature adaptation or growth rate (measured by leucine incorporation) with an overwhelming effect of location and vegetation on this parameter (Rinnan et al. 2009).

Another recent study subjected soils to OTC warming and nutrient addition at one northern maritime (Wynn Knolls, Signy Island) and one southern maritime Antarctic location (Mars Oasis) (Dennis et al. 2012). Responses to the warming treatment were not detected at Wynn Knolls, where OTCs increased mean monthly soil temperatures by up to 0.7 °C. At Mars Oasis, however, where OTCs increased monthly soil temperatures by up to 2.4 °C, warming led to 41 and 46 % reductions in the concentrations of Gram-positive bacterial markers in soil to which glycine and tryptic soy broth (TSB) had been applied, respectively, leading to a decrease of 55 and 51 % in the ratio of Gram-positive to Gram-negative markers in these soils (Dennis et al. 2012). These data suggest that warming may constrain the responses of bacterial communities to carbon and nitrogen inputs arising from dead plant matter entering maritime Antarctic soils in future decades (Dennis et al. 2012).

In the Dry Valleys, no significant effect of warming and wetting on cotton strip decomposition was observed in field manipulations (Treonis et al. 2002). In contrast to moist maritime Antarctic soils, soil processes in the Dry Valleys appeared to mainly be limited by the very low moisture content and this limitation constrains any response to improving environmental conditions (Treonis et al. 2002).

In contrast to some Antarctic soils, bacterial biomass in Arctic soils was reported to be virtually unaffected by artificially increased temperature (Jonasson et al. 1999; Ruess et al. 1999; Schmidt et al. 2002). However, a recent study pointed out that bacteria indeed responded to increased temperature, but that more than a decade of increased temperature was necessary to detect changes in bacterial communities, and that likely even more would be required to elicit a response from fungal communities (Rinnan et al. 2007). It thus appears that some Antarctic environments may respond more rapidly than Arctic environments and that the difference in response time might be related to the relative trophic simplicity of Antarctic environments. Another source of disparity between northern and southern polar regions is that Antarctic climates are far more severe than northern climates at similar latitudes (Convey 2001). Antarctic terrestrial environments also have a much greater degree of physical isolation.

13.4.2 Laboratory Experimental Manipulation

Several studies included both field manipulations and laboratory incubation of soils. In most cases, the laboratory experiment induced larger changes in microbial communities since the magnitude of the change imposed was larger. For instance, Dry Valleys soils did not respond to field manipulation, but laboratory incubation of microcosms, in which soil moisture was increased to 10 % (as compared to 0.6 %), led to increased soil respiration, nitrification and cotton strip decomposition (Treonis et al. 2002). Similarly, an increase of 4 or 8 °C in laboratory incubation led to higher organic matter breakdown, as compared to a lack of response during field warming (where experimental temperatures were increased by <1 °C) (Bokhorst et al. 2007a). These studies suggest that substantial changes are required before significant effects can be detected, and these are often well above the magnitude of the change that is expected to occur in reality.

Global warming will not only raise average temperatures, but also decrease the frequency of freeze–thaw cycles (FTC) at several Antarctic locations. Yergeau and Kowalchuk (2008) sought to contrast the effects of temperature and FTC by using two sets of microcosm experiments. Results showed that bacteria were more affected by warming than by changes in FTC frequency, while fungal community structure and abundance was mostly influenced by FTC frequency and the presence of vegetation (Yergeau and Kowalchuk 2008). The relative densities of several bacterial gene families involved in key steps of the N-cycle were affected by FTCs, while warming had little or no effect (Yergeau and Kowalchuk 2008). FTCs and incubation temperature also significantly influenced laccase enzymatic activity in soil (Yergeau and Kowalchuk 2008).

An interesting study looked at the interactive effects of bacterial predator flagellate species loss and temperature on the abundance of bacteria and the concentration of ammonium in the growth media (Newsham and Garstecki 2007). After 252 h, bacterial abundance was reduced by 75 % and NH_4 concentrations doubled in mixtures inoculated with six and four flagellate species, compared with those inoculated with two species, but only in warmed microcosms. This difference in response was apparently largely owing to the absence of *Bodo saltans* and *Spumella putida*, species with high grazing activities and growth rates, from most replicates of the warmed two species mixtures. The authors concluded that random species loss from food webs or communities is likely to alter the responses of bacteria to environmental change, largely owing to interspecific differences in responses to change (Newsham and Garstecki 2007).

13.5 Conclusions

In summary, despite the interesting findings of previous studies, it is difficult to specifically predict the effects of warming on Antarctic soil microorganisms. One reason is the extreme heterogeneity of soil habitats in this region, as they vary from moist eutrophic ornithogenic soils to nutrient- and water-limited Dry Valley soils. Climate change might have rapid and direct effects on soil microbes that are not otherwise limited, but the release of other limitations (e.g. water, nutrients) could be more important in several environments. In these environments, the indirect effects of climate change through the modulation of plant and bird communities are likely to be more important than the direct effects of climate change for microbial communities. Some interesting approaches could be useful to further increase the knowledge that was presented in this chapter: (1) a longer-term field experiment with factorial manipulation of temperature, nitrogen and water at various locations would help disentangling the relative effects of nutrient and water limitations versus warming; (2) monitoring soil microbial communities in a range of Antarctic environments for a long period of time would be helpful in revealing shifts in natural microbial communities due to ongoing global warming, analogous to what has been done for vascular plant communities (Fowbert and Smith 1994; Smith 1994; Convey 2003); (3) increase the use of high-resolution state-of-the-art molecular methods such as metatranscriptomics and metagenomics which may reveal subtle changes in microbial communities that would otherwise be undetectable. However, following the evidence presented in this chapter, it can already be said quite confidently that in the long run, global warming will have profound effects on Antarctic soil microorganisms.

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Chapter 14
Threats to Soil Communities: Human Impacts

Kevin A. Hughes

Abstract Antarctic terrestrial habitats are vulnerable to impacts resulting from global and local human activities. Global activities have resulted in climate change affecting parts of Antarctica, stratospheric ozone depletion over the continent and dispersal of pollutants to the poles. Local impacts were initiated with the first arrival of humans on the continent in the early twentieth century, but became more widespread with an increase in human activity and footprint from the 1950s onward. Currently, over 30 nations are active in scientific research in the region, more than two million tourist landings have been made, and human visitation is unlikely to decrease. Terrestrial communities are vulnerable to damage or destruction caused by construction projects, vehicle movements and human trampling. Soils have become contaminated with chemicals leaching from waste dumps, and past and current fuel spills have lead to hydrocarbon pollution, particularly near research stations. Terrestrial ecosystems are also under threat from non-native plants, animals and microorganisms introduced inadvertently by historic industries, national operators and the tourism industry. The 'Protocol on Environmental Protection to the Antarctic Treaty' sets out minimum standards of environmental practice for Parties operating in Antarctica. The legislation has gone some way in reducing local environmental impacts, but there is clear evidence that the rigour with which it is applied is not consistent within the continent.

14.1 Introduction

Antarctica is susceptible to the consequences of human activities occurring both globally and locally within the region. In some examples, global activities have resulted in enhanced levels of environmental impacts compared with temperate or

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equatorial latitudes. Radioactive, organic and metal pollutants, transported globally over long distances by air currents, can accumulate in species within higher trophic levels (Pourchet et al. 1983; Bargali 2005). Release of substances that catalyse depletion of the stratospheric ozone layer, such as chlorofluorocarbons (CFCs), has resulted in enhanced levels of short-wavelength UV radiation reaching high southern latitudes during the austral summer, with negative impacts on marine and terrestrial ecosystems (Convey 2006). Climate change, particularly the rapid increases in annual mean temperatures over the western Antarctic Peninsula, is linked with glacier retreat and altered precipitation patterns (Turner et al. 2009). Climate change impacts upon soil communities may be both positive (through increased water availability and temperatures) or negative (through altered radiation levels, local cooling, freeze–thaw event frequency, changes in wind characteristics, precipitation or the occurrence of extreme events), often depending upon the physical and climatic characteristics of specific locations (Convey et al. 2009).

When compared with other populated areas of the globe, the amount of human activity in Antarctica as a whole is low. However, due to the unique physical characteristics and history of human colonization of the continent, impacts may be locally severe and, in particular, present a substantial threat to terrestrial soil communities. Antarctica has an area of c. 14,000,000 km^2 and is the fifth largest continent on Earth. Nevertheless, only c. 44,000 km^2 (0.34 %), an area roughly equivalent to the size of Denmark, is free of permanent ice. Antarctic soils were free of direct human impacts until 1819 when sealers first landed on the South Shetland Islands, Antarctic Peninsula, and commenced their unregulated slaughter of the fur seal and southern elephant seal populations. Other than the remains of their stone refuges and rare artefacts, little evidence remains visible of their activities or their impacts on terrestrial habitats. However, we know little concerning their potential introduction of non-native soil species, or if these species have had impacts on the indigenous soil communities or resident flora and fauna. Following the sporadic presence of sealers in the Antarctic Peninsula region during the nineteenth century, the human footprint expanded with the ‘Heroic Age’ of Antarctic exploration, which extended from the end of the nineteenth century to the early 1920s, and saw the expeditions of Shackleton, Scott, Amundsen, Mawson and Shirase, among others (Headland 2009).

Early expeditions expanded our knowledge of the biology, geology and geography of Antarctica, but the continent remained largely free of human impacts. This was to change with the advent of the International Geophysical Year (IGY 1957/1958) which focussed international scientific attention on Antarctica. Several nations established permanently manned research stations, situated predominantly on coastal ice-free ground, but also on the continent’s fringing ice shelves and the ice cap itself (including Amundsen-Scott Station at the South Pole). Substantial levels of international cooperation abounded during what was the height of the Cold War and led to the drafting and signing of the Antarctic Treaty by 12 original signatory nations in 1959. The Treaty, which entered into force in 1961, demilitarized the region, placed sovereignty claims into abeyance and encouraging scientific cooperation within Antarctica. However, it had little to say on environmental protection and, between the late 1950s and 1980s, considerable disruption of Antarctic habitats resulted from poor environmental management practices. These included waste disposal and the largely unrestricted construction of research stations, roads and other infrastructure. In 1998, the Protocol on Environmental Protection to the Antarctic Treaty (also known as the Environmental Protocol or Madrid Protocol) came into force, which established minimum standards for environmental practice within the Treaty area.

The expansion of human footprint within the continent continues with around 118 facilities currently existing including year-round and summer-only stations, runways and regularly used field camps (COMNAP 2012). Around 50 % of these facilities are concentrated in the ice-free ground of the northern Antarctic Peninsula and associated archipelagoes, and the remainder in the Ross Sea region and coastal oases of East Antarctica. Only six stations are currently situated on permanent ice and therefore do not impact directly upon terrestrial ecosystems. While the global economic downturn may have encouraged national operators to cooperate to reduce cost, India and Korea have recently expanded their footprint in Antarctica with the construction of new permanently manned coastal stations. Of Antarctica's ice-free ground, only c. 6,000 km^2—considerably less than the area of the Galápagos National Park—is within 5 km of the coast. Yet it is here that the majority of the continent's terrestrial plant and invertebrate life and much of its marine vertebrate fauna is found, alongside most of the research stations, runways and docking facilities of the 30 or so national operators with permanent infrastructure in the region (Hull and Bergstrom 2006; Tin et al. 2009). With appropriate coastal locations at a premium, terrestrial habitats and communities in this small area are continually put under pressure by the expansion of human footprint (Hughes et al. 2011a; Cowan et al. 2011, 2012a). The tourism industry is the other main source of human impact within Antarctica today. At its height in 2007/2008, over 33,000 tourists landed in Antarctica although numbers then temporarily declined following the global economic downturn before starting to rise once more (IAATO 2012). The tourism industry is concentrated within the northern Antarctic Peninsula, and the majority of landings now occur at around 30 sites, some of which record over 16,000 visitors during a summer season (e.g. Port Lockroy, Whalers Bay and Neko Harbour) (Lynch et al. 2010).

14.2 Present Legislation on Environmental Protection in Antarctica

The legal basis for the conservation of Antarctica, including Antarctic terrestrial soil environments, is contained within the instruments of the Antarctic Treaty System. The Antarctic Treaty currently has 29 Consultative Parties and 21 Non-consultative Parties. Consultative Parties manage the Treaty area and make decisions during the annual Antarctic Treaty Consultative Meeting (ATCM).

Environmental legislation is contained predominantly within the Environmental Protocol, which designates Antarctica as a 'natural reserve, devoted to peace and science.' This prohibits all activities relating to exploitation of Antarctic mineral resources and sets out basic principles for the conduct of human activities within the Treaty area. The Protocol established the Committee for Environmental Protection (CEP), which provides expert advice to the ATCM on environmental matters.

The Protocol has six Annexes, five of which concern terrestrial habitats. Annex I establishes that an Environmental Impact Assessment (EIA) will be performed for all activities within Antarctica, with the level of EIA dependent upon whether the activity is likely to have 'less,' 'no more than' or 'greater than' a 'minor or transitory' impact. Proposed activities may be approved on the condition that appropriate mitigation measures are put in place. Annex II 'Conservation of Antarctic Fauna and Flora' makes mandatory the granting of a permit by an appropriate national authority before native flora and fauna can be taken or interfered with. It largely prohibits the intentional introduction of non-native plants and animals and states that Parties should also take precautions to prevent the introduction of microorganisms and that the importation of non-sterile soil is to be avoided. The important issues of unintentional importation of non-native species into Antarctica and the intra-regional transfer of non-native species within Antarctic are not specifically addressed in Annex II. Annex III deals with waste generated by Antarctic operations. Sewage and grey water can be disposed of into the sea, ice shelves or ice sheets if no other practical alternative exists, but not onto ice-free areas or into freshwater systems. Open burning of waste and dumping are not permitted and waste is to be stored in such as way as to prevent its dispersal into the environments (e.g. by wind). Waste generated by field camps should also be removed if practicable.

Legislation relating to 'Area Protection and Management' within the Treaty area is laid out in Annex V, with the establishment of Antarctic Specially Protected Area (ASPA) and Antarctic Specially Managed Area (ASMA) classifications. ASPA designation is the highest level of area protection currently possible within the Antarctic Treaty area, with entry to an area conditional upon a permit being granted by an appropriate national authority and the management plan for the area being followed. ASPAs can be designated to protect one or a combination of environmental, scientific, historic, aesthetic and wilderness values. There are currently 73 ASPAs, 65 of which contain ice-free ground with a total area of c. 727 km^2. Currently, seven ASMAs have been established, to assist in the planning and coordination of activities, avoid possible conflicts, improve cooperation between Parties and minimize environmental impacts (e.g. ASMA 2: McMurdo Dry Valleys, ASMA 4: Deception Island).

Annex VI, which has yet to come into force, sets out legislation concerning allocation of liability, should an environmental emergency occur and, although not stated specifically, is most suited to emergencies concerning pollution events at sea and on land. The Annex contains Articles on preventative measures, contingency planning, response action and recovery of costs. However, for terrestrial environmental emergencies, liability is limited to three million Special Drawing Rights (currently c. 4.5 million US dollars). Given the complexities and often long duration of remediation in Antarctic terrestrial environments, this sum may not be adequate to clean up a major spill.

14.3 Physical and Chemical Impacts

Antarctic soils are generally most vulnerable to human impacts during the construction of research stations, roads, runways and other large-scale infrastructure. Construction may destroy soil structure or necessitate the removal of the top layer altogether and leave little opportunity for recovery due to ongoing use (Campbell and Claridge 1987). Careful long-term planning of station construction could minimize impact; however, this does not always occur. For example, Bharti Station was recently constructed outside the recognized 'facilities zone' designated in the ASMA 6 Larsemann Hills management plan, on ground that contained, until then, unimpacted soils within the catchment of scientifically valuable lakes. Once constructed, research station footprints tend to expand over time, often in an unregulated manner and not always subject to environmental impact assessments, resulting in further impacts on Antarctic soils (United Kingdom et al. 2005; Kennicutt et al. 2010).

Local extraction and removal of sand and gravel for building purposes may result in damage to soils and vegetation and generate a permanent alteration of the landscape (Peter et al. 2008; see Fig. 14.1a). Soils may also be vulnerable to damage due to the use of vehicles away from designated roads, which can result in deep trenches in the soil and permafrost, erosion of slopes, alterations of drainage patterns and production of quagmires (Harris 1991). At Fildes Peninsula, King George Island, South Shetland Islands, the increased use of four-wheel 'quad bikes,' for scientific and leisure purposes, permitted access to areas that had not previously been affected by vehicles (Peter et al. 2008; Fig. 14.1b). Even low levels of trampling by humans can result in increased soil compaction and reduced soil faunal diversity, vegetation height, cover and species richness, soil moisture content and porosity (Campbell et al. 1998; Ayres et al. 2008; Tejedo et al. 2009). In low biomass and biodiversity systems, such as the Victoria Land Dry Valleys soils, as few as 20 passes may lead to track formation that can remain visible for many years. In these systems, use of 'sacrificial' tracks rather than dispersal of trampling over the landscape can reduce trampling impacts overall. Recently, trampling impacts caused by tourists have come under greater scrutiny following reports to the ATCM of trampling of moss communities at Barrientos Island, Aitcho Islands, South Shetland Islands, which resulted in the establishment of a moratorium on visitation to the central part of Barrientos Island at least for the 2012/2013 season (ATCM XXXV, Resolution 5).

Local chemical pollution of the Antarctic terrestrial environment has a history as long as human presence on the continent (Kennicutt et al. 2010). Pollution is

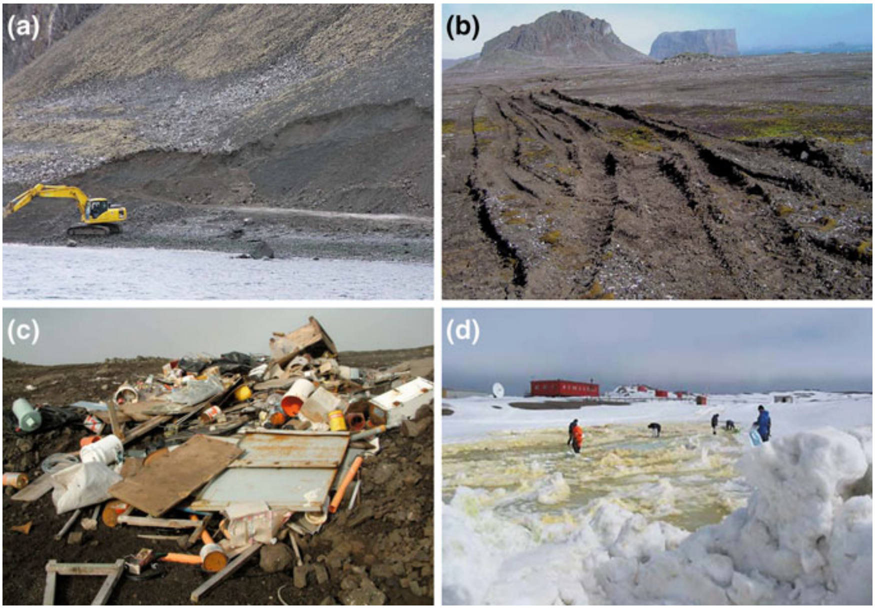

Fig. 14.1 Examples of human impact on terrestrial ecosystems within Antarctica (taken with permission from Peter et al. (2008); Available at http://www.umweltdaten.de/publikationen/fpdf-l/3478.pdf). **a** Quarrying activities leading to the destruction of lichen habitat and storm petrel breeding ground (Photographer: H.-U. Peter). **b** Vehicle tracks over vegetated ground away from the designated road network (Photographer: O. Mustafa). **c** Open dumping of waste near a station (the photograph was taken during the 2003/2004 season, but the dump was still present eight years later; Photographer: C. Buesser). **d** An oil spill on snow-covered ground, with station personnel attempting to remove the oil-impregnated snow (Photographer: Bellingshausen)

often a legacy of earlier waste dumping, both on land and into the sea. Oil and chemical spills that occurred during the establishment and operation of Antarctic facilities since the 1950s (e.g. the abandoned waste dump at Wilkes Station, East Antarctica) are still in need of active management. Earlier poor environmental practices improved in the 1980s and today the Treaty Parties have agreed to conform to legislation laid out in the Environmental Protocol, as a minimum standard. Nevertheless, estimates put the quantity of contaminated soil in Antarctica at between 1 and 10 million m^3 (Snape et al. 2001).

The Environmental Protocol prohibits dumping of waste within the Treaty area although evidence suggest that such activities may still occur on at least a small scale (see Fig. 14.1c). Existing waste dumps can be sources of pollutants including aliphatic and aromatic hydrocarbons, heavy metals, polychlorinated biphenyls (PCBs), antifreezes and other persistent organic pollutants such as the flame retardant poly-brominated diphenyl ethers (PBDE) (Bargali 2005; Hale et al. 2008; Tin et al. 2009). These pollutants may impact upon soil biodiversity in the immediate vicinity and also affect adjacent water bodies through contaminant leaching. Ongoing activities can also release contaminants; for example, the combustion of hydrocarbons (in vehicles, aircraft and generators) and incineration of waste can cause air pollution (Boutron and Wolff 1989). The release of cement dust during building works can result in localized damage to plant communities and alkalization of soils, thereby altering their physiochemical properties and microbial activity through impacts on enzyme efficiency (Adamson et al. 1994).

Given that all Antarctic national operators and the tourism industry rely heavily on hydrocarbons to supply power for their activities, fuel spills are a major potential threat to Antarctic marine, littoral, lacustrine and terrestrial ecosystems. The most significant oil spill in Antarctica occurred at sea with the sinking of the ‘Bahía Paraíso’ and loss of 600,000 l of diesel off Palmer Station, Antarctic Peninsula, in 1989. Onshore, another 260,000 l of fuel was spilled from ruptured bladders at Williams Field on the Ross Ice Shelf, 13 km from McMurdo Station in the same year. No equivalent large-scale spill has yet occurred on ice-free ground (Wilkness 1990; Kennicutt et al. 1991). Smaller spills, caused by the puncture or corrosion of 205-l fuel drums, fuel leaks from vehicles or spills during bulk fuel tank refilling, may be relatively common (Kerry 1993) (Fig. 14.1d). Depending upon the scale and circumstances of the spill, it is likely that some of these incidents may go unreported and not be adequately cleaned up, leading to low level but ongoing pollution of Antarctic soils and ice-free ground around stations and in the field. Acknowledging the risks associated with fuel spills, many nations have contingency plans in place and clean-up equipment near fuel storage areas (COMNAP 2008).

Following a spill, the fate of the fuel will depend upon the characteristics of the contaminated ground, which may change with the season. Depending upon the presence and depth of a permafrost layer, spilled fuel may remain near the surface or disperse to lower levels where it may remain indefinitely. Spilled fuel can change soil properties by altering gas transfer into the soil and increasing its hydrophobicity. Generally, volatile fuel fractions disperse quickly, leaving longer chain hydrocarbons and relatively incalcitrant polyaromatic hydrocarbons (PAHs), which may persist, unaltered, for decades. Hydrocarbons may be toxic to many soil organisms, but also provide a carbon source for some microbial species (Aislabie et al. 2001). Many Antarctic soils contain at least a small proportion of microbial species capable of degrading long-chain hydrocarbons at low temperatures, and the addition of fuel (effectively a novel carbon source) to low carbon and nutrient-limited soils may increase the proportion of hydrocarbon-degrading microorganisms in the population (Kerry 1990; Aislabie et al. 2001). Enhanced by adequate provision of liquid water, long-chain hydrocarbons may be readily metabolized; however, due to enzymatic constraints, PAHs may be less readily degraded leading to their long-term persistence and staining of soil substrate.

Removal of local pollution sources may cause severe damage to existing ecosystems through reactivation and mobilization of contaminants. This is recognized by the Environmental Protocol, which does not require removal of wastes if greater adverse impact would occur than if the waste was left in situ. Some operators, and the Australian Antarctic Division (AAD) in particular, have investigated physical barrier methods to prevent mobilization of contaminants and microbial bioremediation of contaminated ground using techniques such as biostimulation (addition of nutrients), thermal bioremediation (to increase liquid water availability and increase microbial activity), and bioventing (to increase aeration of soils) (see Filler et al. 2008, and reference therein).

14.4 Non-indigenous Species

At any given time, soil community composition is determined by the balance between species extinction and new colonization events. Many factors can play a role in these processes, for instance, extinction can result from changes in climate, water availability or by destruction of habitat by, for example, expansion of ice cover, melt water or volcanic activity (Convey et al. 2008, 2009), and colonization occurs through natural events, facilitated by wildlife, wind and water transport (Hughes et al. 2010). The arrival of humans to Antarctica added an additional vector for transfer of non-indigenous organisms, with species transported in association with personal clothing, cargo, ships, aircraft and foodstuffs (Frenot et al. 2005; Whinam et al. 2005; Lee and Chown 2009a, b; Hughes et al. 2010; Hughes et al. 2011b). Several examples of non-native microbial introductions to Antarctica exist, but little is known of how or even if non-native microbes have altered soil community structure and function. Potentially, soil systems may be impacted by introduced microorganisms altering soil community diversity, structure and function or by non-native macrobiota (e.g. vascular plants and invertebrates) affecting soil chemical and physical characteristics, which, in turn, may affect the composition and structure of the indigenous microbial communities. Introduced microorganisms could also cause disease in indigenous macroscopic organisms.

Airborne microorganisms, of likely human origin, have been detected in and around Antarctic research stations using culture and molecular techniques, suggesting that these can act as a permanent source of non-native microbial species (Pearce et al. 2009). Cowan et al. (2011) estimated that a typical field camp of six individuals occupying an area of 50 m^2 for 10 d could shed c. 6×10^{10} cells, which may represent between 0.1 and 10 % of the natural soil microbial load. Cameron et al. (1977) investigated impacts associated with human activities around McMurdo Station, field camps and in particular the Dry Valley Drilling Project (DVDP). At field camps, contaminants included previously undetected moulds, *Penicillium* species, spore-forming bacteria and, in association with the DVDP, 51 bacterial species were listed as possibly introduced species. Fungal introductions have been recorded in association with fresh (Cameron et al. 1977; Hughes et al. 2011b) and canned foods (Cameron 1972).

Non-native lichens and non-lichenized fungi have been imported on untreated timber (Osyczka 2010; Osyczka et al. 2012), while *Phialophora fastigiata* may have been introduced to disturbed ground and originated possibly from imported wooden boxes (Kerry 1990). Furthermore, the common fungal fuel contaminant, *Hormoconis resinae*, has only been isolated from Antarctic soils that have experienced substantial human impacts including oil spills (Kerry 1990). Non-indigenous algae, previously unrecorded from Antarctica, have been found on boots, fresh vegetables and equipment imported to Scott Base (Ross Sea region) and Maitri Station (Schirmacher Oasis, Dronning Maud Land) (Broady and Smith 1994; Shukla et al. 2006). In the absence of other similar studies or any form of routine biosecurity monitoring, such inadvertent imports are likely to be far more widespread than are currently documented.

The intentional and unintentional transfer of non-sterile soil to the Treaty area from outside Antarctica has been reported on many occasions near research stations, although it is banned specifically by the Environmental Protocol (Smith 1996; Shukla et al. 2006). For example, over 132 kg of non-Antarctic soil containing viable non-native vascular plants, bryophytes, micro-invertebrates, nematodes, fungi, bacteria, and c. 40,000 seeds and numerous moss propagules was introduced accidentally to Rothera Research Station, Antarctic Peninsula, on vehicles which had not been cleaned in accordance with standard procedures (Hughes et al. 2010). Estimates suggest that c. 12 % of fresh food items transported to Antarctica have soil associated with them and that approximately 90 different soils, if not substantially more, may be introduced annually by this route, each with potentially thousands of microbial strains new to the Antarctic region (Hughes et al. 2011b). However, it is unclear what proportion of this soil might reach terrestrial environments, as food washings at most coast research stations enter the waste water system and are released into the sea.

Low minimum standards of sewage waste disposal have resulted in nutrient enrichment and microbial contamination of both marine and terrestrial environments over many years (Smith and Riddle 2009; Tin et al. 2009; Kennicutt et al. 2010). In general, sewage effluent and grey water from coastal research stations are disposed directly into the nearshore marine environment or, if there is substantial risk of effluent pipe damage by ice, the littoral zone. However, faecal coliforms in aerosols originating from effluent outfalls may provide an irregular input of non-native microorganisms and genetic material to soils in the local vicinity (Hughes 2003). Several Treaty Parties have now put measures in place specifying that faecal material, and less commonly urine, should be removed from the field and returned for disposal at research stations (e.g. New Zealand, Australia and the UK). However, over many decades, field party personnel and sledge dogs have deposited sewage and/or faecal material across large areas of both ice and ice-free ground in Antarctica. Human faecal material traditionally was buried in shallow ice pits or in soils.

Recently, a decrease in permanent snow cover around nunataks and in coastal regions, linked in particular to climate change around the Antarctic Peninsula, has resulted in faecal material, abandoned depots, toilet pits and dumped waste melting out, in some cases onto ice-free ground (e.g. Hughes and Nobbs 2004). Several studies have shown that faecal microorganisms, including *Bacillus* spp. and actinomycetes, can survive in the Antarctic environment for 80 years or more (Meyer et al. 1963; Boyd and Boyd 1963; Nedwell et al. 1994; Hughes and Nobbs

2004). However, levels of viability are variable; spore-forming bacteria appear more resilient to Antarctic conditions, while non-spore-forming species may be particularly susceptible to damage by UV, desiccation and freeze–thaw stress and lose viability over a period of hours or days (Parker and Martel 2002; Hughes 2003; Boyd and Boyd 1963). Several culture-dependent studies have shown differences in the microbial community composition of soils in pristine locations and those contaminated with urine (Hirsch et al. 1985; Boyd and Boyd 1963) and other human waste around camps and research stations (Cameron 1972; Miwa 1976; Toyoda et al. 1985; Abyzov et al. 1986). Use of molecular techniques has shown the extent of faecal indicators and human commensal bacteria in terrestrial environments, specifically in the Ross Sea region (Sjoling and Cowan 2000). Specific PCR primers revealed *Escherichia coli* DNA at an abandoned camp site at Canada Glacier (occupied from 1976 to 1988), but none were detected at the occupied Lake Fryxell camp (established 1990), which may indicate an improvement in human waste management practices (Baker et al. 2003). Cowan et al. (2011) attempted to assess the risks of non-native microorganism importation into Antarctica concluding that, while introductions are likely and impacts on microbial communities may be minimal, further effort should be made to protected microbial systems from genetic contaminants and biological homogenizations.

Many of the microorganisms introduced to Antarctica are likely to be mesophilic and may not function optimally at the low temperatures that occur predominantly in Antarctic terrestrial habitats. Antarctic soil temperatures may vary widely over short spatial and temporal scales, and some soils exposed to direct solar radiation may rise to temperatures of >20 °C for periods lasting minutes to hours (Bokhorst et al. 2007). Nevertheless, the contribution of introduced microorganisms to soil biogeochemical processes is likely to be dwarfed by the activities of indigenous soil species which are largely thought to be psychrotolerant and, in general, better adapted to the desiccation, nutrient limitation and freeze–thaw stresses characteristic of polar terrestrial habitats.

One important but unquantified impact that introduced microorganisms may have is the provision of novel genetic material to Antarctic soils, which could in theory persist for long periods under dry, cold preservation conditions typical of some areas of the Antarctic such as the Victoria Land Dry Valleys (Ah Tow and Cowan 2005). Rates of lateral gene transfer by transformation, conjugation or transduction are likely to be low in dry soils, but could occur within microbial biofilms that can form on soil particles and show enhanced water retention through the production of extracellular polysaccharides. The introduction of novel genetic material may alter the evolution of native microbial communities, but normally for the DNA to be retained it must confer a selective advantage to the species that has taken it up, such as through antibiotic resistance, novel degradative pathways or secondary metabolite production (Cowan et al. 2011).

Information on the introduction of macroscopic species and their consequences is increasing (Frenot et al. 2005). However, in general, little consideration has been given to the effects these species may have on indigenous soil microbial communities. Chown et al. (2012b) undertook a continent-wide evaluation of the risks to Antarctica posed by non-native vascular plants by quantifying the input of seeds and plant propagules into Antarctic on visitors' clothing. Scientists and tourist support staff were found to carry more seeds than tourists or ships' crew. The areas of Antarctica considered at greatest risk of introductions were those experiencing significant human activity on the western Antarctic Peninsula (especially the South Shetland Islands), with the Ross Sea region and coastal oases of East Antarctica at risk to a lesser degree. These areas are also likely to be at risk of invertebrate and soil introductions. These predictions are supported by recent reports of introduced vascular plants and six species of Collembola on Deception Island (South Shetland Islands), which is one of the most visited locations in Antarctica (Greenslade et al. 2012; Smith and Richardson 2011).

The non-native grass, *Poa annua*, is now known to be present in two locations in the western Antarctica Peninsula (Molina-Montenegro et al. 2012). It is most widespread near Arctowski Station, King George Island (South Shetland Islands), where it was introduced originally in c. 1984/1985 and has now spread over 1.5 km to the exposed foreground of the retreating Ecology Glacier within ASPA 128 Western Shore of Admiralty Bay (Olech and Chwedorzewska 2011). *P. annua* has been shown in greenhouse studies to have negative impacts upon the two native Antarctic vascular plants, *Deschampsia antarctica* and *Colobanthus quitensis* (Molina-Montenegro et al. 2012). If eradication or containment measures are not put in place, *P. annua* may disperse further with potentially large impacts on coastal soil communities in the Antarctic Peninsula region and possibly beyond as climate change continues (Chown et al. 2012b). Similarly, the impact of the non-indigenous flightless chironomid midge, *Eretmoptera murphyi*, may also increase considerably. With mean populations that have now increased to 21,000 larvae m^{-2} in soils within its current distribution at Signy Island, South Orkney Islands, this species could increase annual litter turnover by nine times compared with estimates for the indigenous microarthropods (Collembola and Acari). This would have substantial impacts upon the indigenous microbial population (Hughes et al. 2012).

14.5 Conclusions

The Antarctic Treaty Parties, and their environmental managers, are faced with the challenge of facilitating ongoing human activity within the region, but concurrently minimizing impact upon the environment. With the exception of the 'ozone hole,' which is predicted to repair within the next century, Antarctica is likely to continue to be vulnerable to all of the human impacts discussed here. Some attempts have been made to predict future environmental issues of concern and to encourage necessary research to help mitigate against potential impacts (Chown et al. 2012a). Given the diversity of activities undertaken in Antarctica, the expanding human footprint and the increase in construction of logistic facilities, this will be a major challenge, made all the more difficult because information on past activities and cumulative impacts is not readily available. The Environmental

Protocol was signed over 20 years ago and has resulted in improved environmental practice compared with earlier times. However, terrestrial habitats continue to be threatened by human activity and, even without the development of further legislations, could be better protected today by more comprehensive and effective implementation of the Protocol.

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Chapter 15
Antarctic Climate and Soils

Peyman Zawar-Reza and Marwan Katurji

Abstract Climate change is having a significant impact on the ecosystems of Antarctica and has been the focus of scientific research in the past few decades. Our understanding of how large-scale weather patterns have changed has increased, but there is still way to go before we know how the shift in climate influences temperatures at microscales. Antarctica has one of the most severe climate extremes on the planet; it is the windiest, coldest, and driest. Combined with its geographic isolation, observational studies of climate change have been hampered due to lack of sufficiently dense monitoring systems. The soil exchanges energy with the overlying atmosphere (boundary layer) which influences its temperature through sensible and latent heat fluxes, both are poorly understood in the terrestrial landscapes of Antarctica. It has been shown that at least at the height of biological activity during summer, shifts in weather patterns across the Dry Valleys can have profound impacts on temperature and availability of liquid water, with downstream consequences for the biota. Therefore the terrestrial ecosystem responds rapidly to the larger climate system on a seasonal timescale.

15.1 Climate of Antarctica

Evidence continues to accumulate that climate change is having a profound impact in the Earth's cold regions; the impact on surface temperature has been more severe in the Arctic. The stratospheric ozone depletion, however, has been the flagship of anthropogenic influence on the Antarctic continent, with the increase in temperatures not as dramatic as the Arctic. Long-term monitoring of sea-ice extent, glacier mass balance, ocean temperature and circulation, permafrost, and air temperature

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indicate that concerns about pronounced warming in polar regions raised more than two decades ago by general circulation modelling experiments (e.g. Manabe et al. 1991) were well founded. Commenting on scientific findings, the intergovernmental panel on climate change (IPCC) fourth assessment report (AR4) stated with high confidence 'that natural systems related to snow, ice and frozen ground (including permafrost) are affected'. Examples include enlargement and increased numbers of glacial lakes, increasing ground instability in permafrost regions, and changes in some Arctic and Antarctic ecosystems (Pachauri and Reisinger 2007).

Antarctica has a vastly different climate regime when compared to the Arctic. Most opening paragraphs on Antarctic climate begin by stating that 'Antarctica is the coldest, windiest and driest continent on Earth'. These characteristics are explained by the continent's geographical location (which determines how much solar radiation it receives), the fact that it has the highest average elevation, and the effect of the uninterrupted Southern Ocean isolating the continent's atmosphere. A comprehensive survey of knowledge on Antarctic climate was recently published by Scientific Committee on Antarctic Research (SCAR; Turner et al. 2009), covering not only the climate system in deep historical time (thousands of years into the past), but also the contemporary climate linkages with the global climate system (via tele-connections). This report was superseded lately to include new findings (Turner et al. 2013). Naturally, most climate research focuses on the spatial and temporal characteristics of either the snow/ice-covered regions of the continent, or the vast and dynamic sea-ice sheet that surrounds Antarctica, in this chapter; we will only examine the exposed soil regions.

Studies into climate (change) of Antarctica have been primarily hampered by paucity of in situ data. Despite the increase in the number of automatic weather stations (AWS) in the last 30 years, which stands at approximately 68 (Lazzara et al. 2012), spatial interpolation is often performed to map out geographical variation in unobserved areas. This is achieved by blending-in other data sets (such as remote sensing or numerical weather prediction data). Plans are in place to increase the amount of monitoring points, yet the harshness of the environment, and the logistical difficulties hamper efforts.

To extract climate signals, long-term records are needed, yet only a handful of AWS have operated for more than two decades; barely long enough to establish a significant trend (Schneider et al. 2011). When combining records to make a reconstruction, assumptions need to be made concerning selection criteria for the input data and the statistical methods to be used. Even with the generally large spatial coherence and correlation length scales of temperature anomalies at polar latitudes (e.g. Hansen et al. 1999; Chapman and Walsh 2007), none of the reconstruction methods can escape the basic limitation of few in situ observations in West Antarctica, and all exhibit less skill in this region compared with other regions of the continent, mainly due to the high variability in topography.

We have learned a great deal about the climate of the Antarctic since climate observations began. For the past 50 years, surface temperatures in Antarctica have increased by an average of 0.1 °C/decade (Schneider et al. 2011). But there is significant regional (West Antarctica vs. East Antarctica) variation and distinct

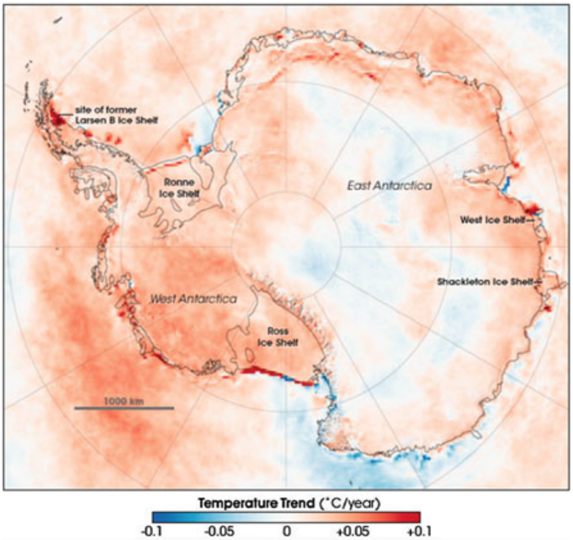


Fig. 15.1 Radiative surface temperature trends between for the period 1981–2007. (*Source*: http://earthobservatory.nasa.gov/IOTD/view.php?id=8239)

seasonality to the trends. East Antarctica has shown insignificant warming trends in summer and autumn (yet perhaps even some cooling), but with warming in spring and winter. In contrast, West Antarctica has experienced significant warming in spring (except for the Peninsula).

What is certain is that climate change signal varies across the continent. Some researches have recognized the enhanced warming in the Antarctic Peninsula (e.g. Rott et al. 1996; Chapman and Walsh 2007), and then on the other hand, Doran et al. (2002a, b) studied the McMurdo Dry Valleys for the period 1986–1999 and concluded that summer temperatures had decreased by 1.28 °C per decade. The autumn temperatures even showed a more dramatic decrease of more than 2.0 °C per decade. For the McMurdo Dry Valleys (MCM) in Victoria Land, Bertler et al. (2004) suggested that the short-term cooling was associated with El Nino-Southern Oscillation (ENSO)-driven changes in atmospheric circulation. In studying the effect of circulation patterns on Antarctic climate from 1957 to 2004, Marshall et al. (2007) reported that parts of the Antarctic continent are cooling. Considering the continent as a whole, AR4 states, 'it is likely that there has been significant anthropogenic warming over the past 50 years averaged over each continent (except Antarctica)' (Fig. 15.1).

The map in Fig. 15.1 is produced from thermal infrared (heat) observations made by satellite sensors. Satellites do not measure air temperatures, but can measure radiative surface temperatures by capturing the heat energy given off (emitted) by the surface. It shows that across most of the continent and the surrounding ocean, temperatures have climbed between 1981 and 2007. In some places, the rate of warming approached a tenth of a degree each year (2 °C over the entire period). Temperature rise was greater and more widespread in West Antarctica than in East Antarctica, where some areas showed little change or even cooled.

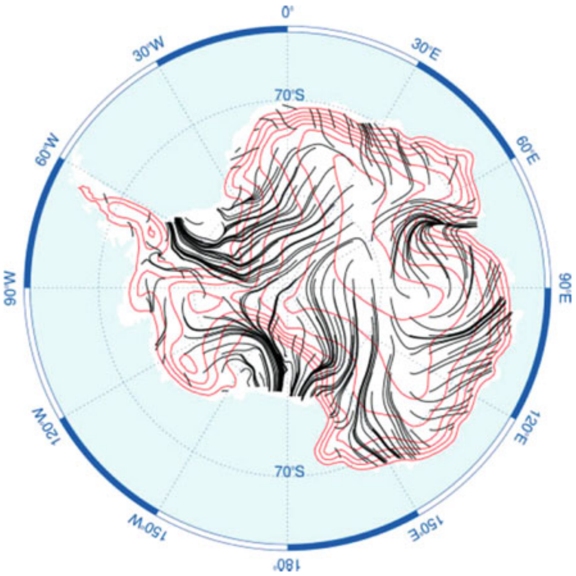


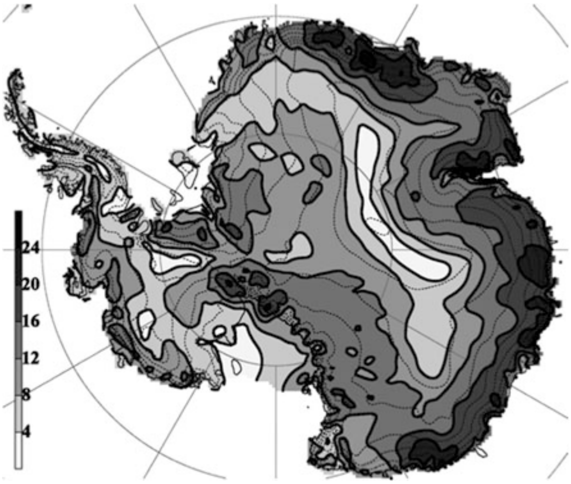
Fig. 15.2 Low-level katabatic wind patterns over the continent (adapted from Van Lipzig et al. (2004))

Antarctica is known for its katabatic winds, which influence the climate of almost the entire continent. Katabatic winds prevail when cold air is formed on a sloping terrain and simply drains towards lower elevation under the force of gravity. The ice/snow-covered sloped terrain produces katabatic winds almost constantly, directed by the topography, a diverging low-level flow pattern is set up (Fig. 15.2). The katabatic winds transport significant mass of air towards the continental margin and are in part responsible for the harsh weather experienced by early explorers.

The 'windiness' aspect of Antarctica is conveyed in Fig. 15.3. This map is produced by a computer weather model showing average annual wind speeds close to the ground. The coastal margins tend to record some of the highest sustained wind speeds recorded on Earth, because as the katabatic approaches the steep coastal topography, it interacts with the storm systems that circumnavigate the Southern Ocean and intensifies. The steeper slopes at the coastal margins, and the convergence of the katabatic through gaps (valleys) in the mountainous terrain also contribute to this intensification. The strength and variability of the katabatic winds can have significant impact on other systems, for example sea-ice. The increased intensity of the katabatic winds was shown to be responsible for the expansion of sea-ice (Holland and Kwok 2012) and is one of the factors in the sea-ice extent reaching its maximum recorded expansion in winter of 2012.

This chapter will focus on the state of knowledge regarding the boundary layer climates of the regions in Antarctica that have extensive areas of exposed soil. The boundary layer is the layer in direct contact with the surface. Exposed rock and soil total only about 46,000 km^2 of continental Antarctica (approximately 0.33 % of the land area) (Fox and Cooper 1994). The exposed soil exchanges energy with the

Fig. 15.3 Annual average wind speeds near the surface in meters per second (adapted from Parish and Bromwich 2007)



atmosphere, so both systems are coupled. To understand the heat flow in the soil, we need a closer examination of how energy is transferred between the two.

15.2 Boundary Layer Climate

Heat conduction into soils is important to understanding potential responses to changes in surface energy balance, particularly in the context of changing climate. Local energy exchange processes and transport of energy due to large-scale weather systems control the air and ground temperatures. During synoptically quiescent periods, the surface energy balance dominates how temperatures evolve in time, whereas in other synoptic conditions (such as storms), the transported air mass can have an overriding influence.

The radiation balance at the surface is defined as:

$$Q^{*} = (K\downarrow - K\uparrow) + (L\downarrow - L\uparrow)$$

where $K\downarrow$ down-welling short-wave solar radiation, $K\uparrow$ is the reflected amount by the surface, $L\downarrow$ is the down-welling long-wave radiation, and finally $L\uparrow$ is the long-wave radiation emitted by the surface. The balance of these components determines the net all-wave radiation balance (Q^*), which is basically the energy available for heating (if the balance is positive) or cooling (if the balance is negative) of the surface. Each of the individual radiative components can be controlled by a variety of complex factors; for example, $K\downarrow$ and $L\downarrow$ are controlled by cloud amount on short timescales, and by latitudinal location on seasonal timescales.

The microclimate is determined by the properties of the surface and how it handles the energy flow. The net all-wave balance is subsequently partitioned through the surface energy balance:

$$Q^* = Q_H + Q_E + Q_G$$

where Q_H is turbulent sensible heat flux, Q_E is the turbulent latent heat flux (both sensible and latent heat fluxes represent the exchange between the surface and the atmosphere) and Q_G is the subsurface conductive heat flux (this component can be either ice/snow or soil). Typically, if Q^* is positive and the surface has surplus of energy, the fluxes tend to flow away from the surface (i.e. the air above the ground gets heated, and if there is water available at the surface it will evaporate). For a more detailed explanation of boundary layer climates see Oke (1987).

The sensible and latent turbulent fluxes are complicated functions of atmospheric stability (state of turbulence) and vertical gradients of temperature and moisture in the atmosphere, but their descriptions are beyond the scope of this chapter. The conduction of energy in the ground is governed by Fourier's law defined as:

$$Q_G = -\lambda\left(\frac{\mathrm{d}T}{\mathrm{d}z}\right)$$

where Q_G at any depth is determined by λ (thermal conductivity of the soil), and the vertical gradient of temperature with depth (d = temperature difference between two levels). Thermal conductivity depends primarily on soil composition and water/ice content. The conduction of energy in the ground therefore is a function of surface energy balance, and energy (heat) can either propagate towards the surface or away from it. For the exposed ground in Antarctica, the ground layer can be broken into an active-layer, and a permafrost layer. The active-layer is underlain by permafrost and is subject to freezing and thawing cycles due to close coupling with fluctuations in atmospheric temperatures (Linell and Tedrow 1981) whereas the permafrost remains at or below 8 °C for more than two years (Linell and Tedrow 1981). The permafrost thermal regime reacts to climate variations at different timescales: (1) seasonally above the depth of zero annual amplitude (ZAA), (2) annually at the ZAA and (3) from years to millennia at progressively greater depths.

Air temperature and snow cover are tightly coupled to permafrost thermal regime and active-layer thickness through the surface energy balance (Guglielmin et al. 2003; Guglielmin 2004; Adlam et al. 2010; Zhang and Stammes 1998). Down-welling solar radiation ($K\downarrow$) can be especially important on bare ground surfaces (Adlam et al. 2010).

Naturally, most observational and modelling research into radiation and surface energy balances in Antarctica has focused on snow/ice-covered regions (King et al. 2006; Van den Broeke et al. 2006; Munneke et al. 2012).

In the MDV, surface energy balance has a stronger influence on the hydrological cycle than precipitation. The hydrological cycle, particularly melting, is controlled by daily, seasonal and annual variation in surface energy balance (i.e. net all-wave radiation, sensible and latent turbulent heat fluxes) (Gooseff et al. 2011). Liquid water can be present at the surface due to surplus of net all-wave energy, which can drive sensible heat and warm local ambient temperature. Despite the 24-h solar radiation, glacier melt can still vary considerably on a diurnal cycle, due to solar elevation and topographic shading.

15.3 Soil Climate Monitoring

Recognizing the importance of monitoring ground temperatures, the scientific community established a network under the auspices of the global terrestrial network for permafrost (GTN-P). Ground temperature is monitored in boreholes in Antarctica with depths ranging from 2.4 to over 125 m. Temperature is monitored and logged at these sites within the active-layer and the permafrost to understand their long-term response under a changing climate. At some Circumarctic Active-Layer Monitoring—southern hemisphere (CALM-S) sites, soil temperature is measured at increments of 10 cm for the upper 1 m, with lower frequencies at depth. For a comprehensive description of the state of active-layer and permafrost monitoring see Vieira et al. (2010). Temporary networks are sometimes established for studies that need higher spatial resolution information. Adlam et al. (2010) established such a network for a 4-year period (1999–2003) in the McMurdo Sound region.

Although the permafrost layer's thermal state is important as a proxy for climate change, it is the active-layer that acts as a conduit for energy and controls heat conduction towards the permafrost layer (Fig. 15.4). The periodic warming pulses that the active-layer exhibits during winter, due to the air temperature pulsation that are controlled by warmer air intrusions from synoptic disturbances or katabatic winds, will propagate towards the permafrost layer and gradually over time increase its pre-summer energy storage making it more vulnerable to the continuous summertime solar radiation and thawing (Fig. 15.4).

Adlam et al. (2010) studied the soil climates in the McMurdo Sound region for a four-year period (1999–2003). The study investigated the active-layer depth for eight summers, but found the deepest active-layer depths occurred at all sites for the warm summer of 2002/2002 (Doran et al. 2002a, b). Therefore, the active-layer responds rapidly to interannual fluctuations in local climate. Yet there was no significant overall trend for the period of study. The duration of this research is probably too short for trend detection. Interestingly, they report that the mean summer and winter air temperatures, the total summer solar radiation, and mean summer wind speed explain 78 % of the variation in the active-layer depth (R^2 0.73).

Soil moisture can also contribute to soil heat conductivity, and although the soils in MDV are extremely dry, a considerable gradient can exit in summer along the many lakes and streams. A soil moisture gradient study adjacent to Lake Fryxell in Taylor Valley was presented by Ikard et al. (2009). They aimed to

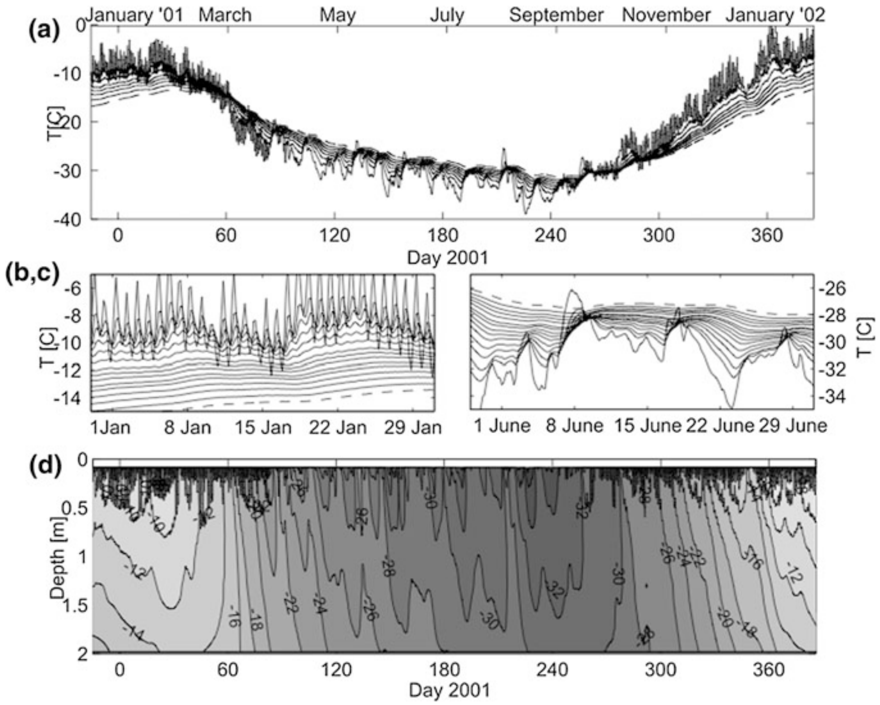


Fig. 15.4 Soil temperature time-series data near Ferrar Glacier in MDV. **a** The *bottom* temperature is at a depth of 1.98 m (*dashed line*) and the top temperature at 0.09 m has the largest amplitude (note: the figure is showing every second thermistor for clarity). **b** Reconstruction of soil temperature field; isotherm increments are 2 °C. From Pringle et al. (2003)

characterize the thermal characteristics of these relatively wet soils (as compared to the rest of the McMurdo Dry Valleys landscape) and to assess the response of the active-layer to possible increases in soil moisture. Estimated bulk ATD values were consistently greater in locations of enhanced soil moisture, so lakeside soils were more likely to conduct energy into the subsurface. Increased soil moisture across the landscape would likely increase ATD, allowing for greater heat exchange between the atmosphere and the subsurface.

Understanding the soil climate in the MDV can also aid in scientific fields such as astrobiology. The growing knowledge and understanding of surface processes on Mars have sparked an interest in the Dry Valleys of Antarctica as one of the closest natural terrestrial analogue of the Martian environment. Ideas and hypotheses can be tested there prior to launching probes into the distant planet, and careful analysis of corresponding periglacial terrestrial environments (Costard et al. 2002) is likely to aid in the interpretation of images gathered by Mars Orbital Imager (Malin and Edgett 2000).

15.4 Climate of the MDV

We consider in this section the state of knowledge regarding the boundary layer climate of the Dry Valleys. The ice/snow-free surface makes the energy exchange between the atmosphere and the ground significantly different from other locations in Antarctica. Although other ice/snow-free regions exist, MDV is by far the most extensive and studied region.

The MDV system is considered to be a polar desert, receiving little precipitation (annual water equivalent of 2–50 mm in the valleys bottoms; Fountain et al. 2010). Due to association with strong winds, precipitation is notoriously difficult to measure in MDV—and indeed in the rest of Antarctica. Little seasonal variability in snowfall is observed, but the spatial gradient can be quite pronounced, with values of 50 mm water equivalent along the coast sharply decreasing to 3 mm further inland (Fountain et al. 2010). The precipitation maximum at the coastal margin of Taylor Valley has been attributed to the winter convergence of local wind regimes that produce localized uplift. Snow patches accumulate as direct precipitation and drifting snow. Accumulation in valley bottom occurs in any wind-sheltered location, behind boulders, microtopographic features and within stream channels. Drifting snow by strong plateau wards wind intrusions, and glaciers account for roughly half of the measured snow accumulation.

Monaghan et al. (2005) investigated the reason(s) for the low precipitation amounts with a weather forecasting model. Using the one-year climatology generated by the model, they placed the MDV in the precipitation shadow region of the Transantarctic Mountains, where the moisture laden air streams from the large synoptic systems passing to the northeast and east of Ross Island do not penetrate the area. Most precipitation is in the form of snow and sublimates into the dry air prior to melting. But melting into ground is possible during summer with warmer ground temperatures and has been observed and modelled (Dallafior et al. 2012). Snow is a critical moisture source to the microbially dominated ecosystems in the soils of the Dry Valleys (Wall and Virginia 1999). Annual averages for air temperature hover near −18 °C, while in winter they dip to −50 °C and for summer a few degrees below 0 °C (Doran et al. 2002a, b).

With ample short-wave radiation, each valley in the MDV can develop its own distinct microclimate regime during the summer (Fig. 15.5). Characterizing the microclimate regimes in the MDV is the aim of New Zealand Terrestrial and Biodiversity Survey (nzTABS) and is achieved by AWS and shallow soil (2 cm) temperature measurements. There are marked variations in microclimates between the valleys; the soil layer can be above freezing point for a significant time in summer, and smaller valleys such as Miers can show significantly warmer monthly temperature (close to 5 °C warmer). Miers is also a much more humid environment as reflected by the higher summer relative humidity.

In addition to the surface energy balance, horizontal transport (advection) of energy by winds is another factor in climate. In MDV, katabatic winds (drainage winds) are a characteristic feature. The larger-scale katabatic winds flow from the

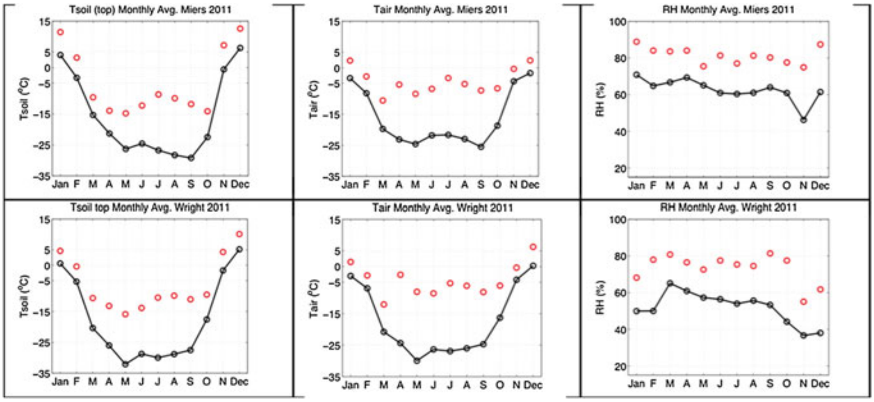


Fig. 15.5 Monthly averages (*black dots*) and the maximum daily value for the month (*red dots*) for Miers and Wright valley (data provided by NzTABS). RH is for air and not soil!

polar plateau at the western edge and can cause significant warming (particularly in winter) as they get adiabatically compressed when descending from higher elevations. They can reach significant intensity and flow above 20 m/s for prolonged periods. Air temperature increases by about 30 °C has been recorded over a few hours. This means that the frequency of these events has a significant impact on average temperatures; as it has been estimated by Nylen (2004) that for every 1 % increase in frequency, summer average air temperatures increase by 0.4 °C and winter average air temperatures increase by 1.0 °C (Fig. 15.6).

The interaction of boundary layer winds and the shallow soil temperature was examined for the Wright Valley by Zawar-Reza et al. (2012). This study looked at the variation of soil temperature with altitude from a series of temperature sensors placed along valley sidewalls for a winter season. The relationship between soil temperature and altitude shows that the valley bottom soils can be significantly cooler in winter—by as much a 15 °C, as cold air is trapped (ponded) by topography. Ridge-top areas are comparatively warmer, but this difference is occasionally obliterated as the strong katabatic winds warm the boundary layer within the valley and the soil.

15.5 Soil Climate and Global Change

The latest update on Antarctic's response to climate change states the likelihood of degradation in permafrost condition, and subsidence of ground surface amongst several other effects (Turner et al. 2013). As the atmospheric boundary layer warms and the surface receives more solar radiation, the active-layer is predicted to thicken. The thickening could have significant impact on terrestrial ecosystems. Areas deemed most susceptible are Antarctic Peninsula and coastal areas in East Antarctica.

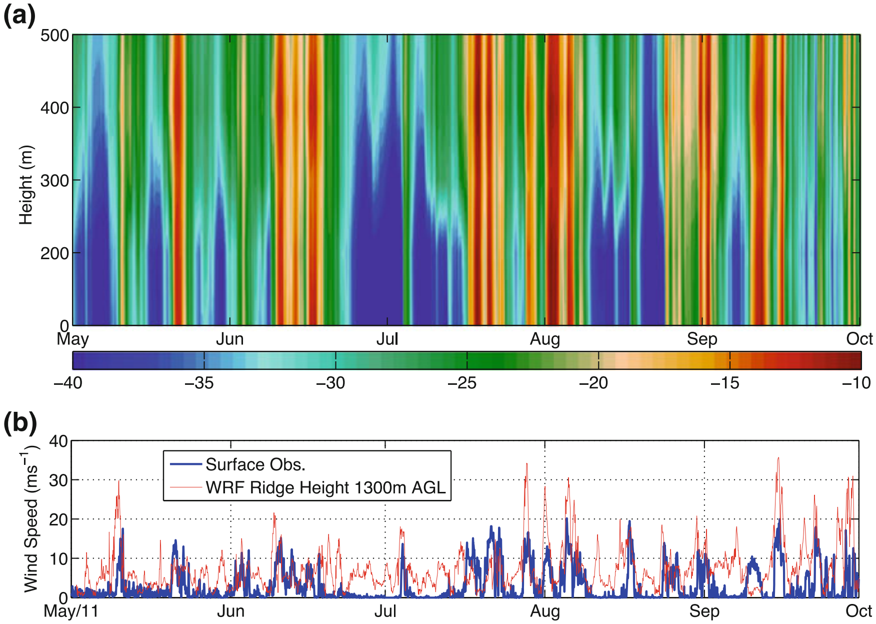


Fig. 15.6 **a** Variation of top soil temperature in winter for wright Valley, **b** linked with modeled and observed wind speeds

The Dry Valleys have cooled by 0.78 °C per decade between 1986 and 2000 as determined from the in situ meteorological data (Doran et al. 2002a, b). This observation is contradictory to the concept of amplified warming in polar regions, and the substantial warming observed in Antarctica's Peninsula region over the second half of the twentieth century. The cooling reported by Doran et al. (2002a, b) is ecologically significant as it was more pronounced in summer (and autumn). The cooling trend is significantly correlated with decreased winds and increased clear-sky conditions, which can probably be attributed to more long-wave radiation loss from the surface. Since winter temperatures are well below the freezing point of water, winters do not have a significant direct impact on the hydrology or ecology. Therefore, summer temperatures are deemed to be critical drivers of the ecological system. The ecological response to the climate cooling included decreased primary productivity of lakes (6–9 % per year) and declining numbers of soil invertebrates (more than 10 % per year).

Later on, evidence was presented that linked the observed cooling to ENSO. ENSO is thought to be responsible for influencing the regional meteorology over the Ross Ice Shelf (Bertler et al. 2004). As a result, the authors challenged the idea that the cooling will be a long-term concern as ENSO exhibits variability on a decadal time scale. It appears that during La Nina events, the low-pressure system north of the Ross Ice Shelf is stronger and advects relatively warm and moist air from the north into the Ross Sea region. During El Nino, this flow is suppressed, as

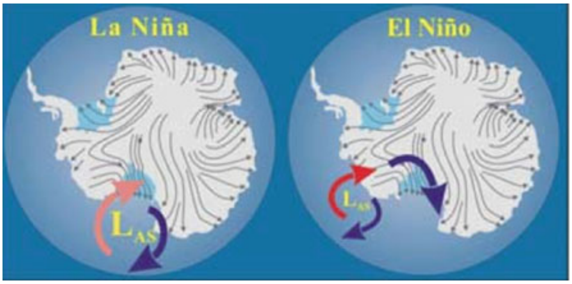


Fig. 15.7 Climatological position of low pressure system in the Ross Sea. (From Bertler et al. (2004))

the low-pressure moves towards Amundsen Sea, forcing colder air masses through Siple Coast (Fig. 15.7).

What will be the specific effects of climate change on ecosystems in Antarctica? One study that addresses this question investigates how two unusual summers—one anomalously warm and the other unusually cold—affected the hydrology and the ecosystems in the MDV (Doran et al. 2008). The study found that changes in large-scale meteorological conditions had a major influence on the average temperatures. The synoptic features of the summer of 2000/2001 directed up-valley flows into MDV (air masses coming from the Ross Ice Shelf into the valleys), causing colder conditions, with an average seasonal temperature of −6.1 °C. In contrast, when the synoptic drivers forced airflow down-valley, with air originating from the East Antarctic Ice Sheet in 2001/2002 season, the valleys recorded much warmer average seasonal temperature (−3.7 °C). Since it was found that the difference in average short-wave radiation was negligible between the two seasons, the horizontal advection was deemed to have an overriding control.

The 2.4 °C difference between the two seasons had a vivid impact, leading to significant glacier mass loss in Taylor Valley and 3,000–6,000-fold increase in streamflows, and also lake levels decreased slightly in the colder summer and increased between 0.54 and 1.01 m with warm conditions. As the authors noted, the warm season erased the prior 14 years of lake level lowering in just three months.

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Chapter 16
Antarctic Soil Properties and Soilscapes

J. G. Bockheim

Abstract Antarctica can be divided into eight ice-free regions that comprise 47,000 km2 (0.35%) of the continent and its offshore islands. Soils, as traditionally defined, cover most of this area. Soils of Antarctica are influenced primarily by regional differences in climate and age of the parent materials. Predominant soil-forming processes include rubification (reddening), salinization/alkalization (accumulation of soluble salts), carbonation, humification, cryoturbation, desert pavement formation, podzolization, permafrost formation, and phosphatization (accumulation of P from bird influence). Soils of Antarctica generally are coarse - textured with abundant coarse fragments (>2 mm) and a predominance of sand in the fine-earth (<2 mm) fraction. Many soils of Antarctica, particularly in the interior mountains, have low moisture contents. Permafrost occurs continuously in Antarctica except in the offshore islands, where it is discontinuous or sporadic. Whereas soils in the interior mountains often contain abundant salts and low levels of organic C and P, soils along the coast generally contain fewer salts and higher levels of organic C and total P. Although weathering processes tend to be slower in Antarctica than in other regions, mineral alteration can be advanced in soils of early Quaternary and older age. About 53% of the soils of Antarctica have been mapped at a reconnaissance scale. Gelisols (permafrost-affected soils) are dominant in most regions of Antarctica, but coastal areas may feature Inceptisols and Histosols. Key soil properties affecting the distribution and abundance of organisms include available water content, duration of the period in which the ground temperature exceeds 0°C, the level of soluble salts, pH, the relative abundance of inorganic and organic N, and the amount of organic C.

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16.1 Background

Only 0.35 % of Antarctica is ice-free. The largest ice-free area is the Transantarctic Mountains (24,200 km^2), followed by the Antarctic Peninsula and its offshore islands (10,000 km^2), with smaller areas (from largest to smallest) scattered around the periphery of the continent in MacRobertson Land, Queen Maud Land, the Ellsworth Mountains, the Pensacola Mountains, Ender by Land, Wilkes Land, and Marie Byrd Land (Fig. 16.1).

The unconsolidated materials in Antarctica are considered soils in that they are natural bodies comprised of solids (minerals and organic matter), liquid, and gases, which occur on the land surface, occupy space, and are characterized by horizons, or layers, that are distinguishable from the initial material as a result of additions, losses, transfers, and transformations of energy and matter (Bockheim 1982). This definition was adopted by the Soil Survey Staff (2010) to replace an earlier definition that emphasized the presence of higher plants.

In that the unconsolidated materials of Antarctica contain soils, they can be differentiated on the basis of standard soil-horizon nomenclature (Soil Survey Staff 2010), and they can be mapped at various scales (Beyer and Bölter 2000; Hofstee et al. 2006; Bockheim et al. 2007, 2008; Bockheim and McLeod 2008).

At the highest scale, soils of Antarctica are influenced primarily by climate and time (Bockheim 2008), with the other soil-forming factors of organisms, relief, and parent material generally being more locally important. There are three predominant climates in Antarctica: a mild-wet-maritime climate along the western Antarctic Peninsula (Region 8 west), a cold-moist-maritime climate along the eastern Antarctic Peninsula (Region 8 east) and East Antarctica (Regions 2 through 4), and a very-cold-hyperarid-inland climate elsewhere in the interior mountain ranges (Regions 1 and 5 through 7) (Fig. 16.1).

In the McMurdo Dry Valleys (MDVs), Marchant and Head (2007) recognized three microclimate zones: a coastal thaw zone, an inland mixed zone, and a stable upland zone; zones are defined on the basis of summertime measurements of atmospheric temperature, soil moisture, and relative humidity. Subtle variations in these climate parameters result in considerable differences in the distribution and morphology of: (1) macroscale features (e.g., slopes and gullies); (2) mesoscale features (e.g., polygons, including ice-wedge, sand-wedge, and sublimation-type polygons, as well as viscous-flow features, including solifluction lobes, gelifluction lobes, and debris-covered glaciers); and (3) microscale features (e.g., rock-weathering processes/features, including salt weathering, wind erosion, and surface pitting) and, hence, soil development. The soil climate, including soil-moisture regime and soil-temperature regime, varies accordingly within these climate zones and impacts soil formation and the distribution of biota.

Figure 16.2 illustrates the type of soils that form in well-drained locations in each of the three predominant climate types. In the mild-wet-maritime climate, the soils tend to be young because of recent deglaciation, and they lack permafrost. In the cold-moist-maritime climate, ice-cemented permafrost is apparent and there is

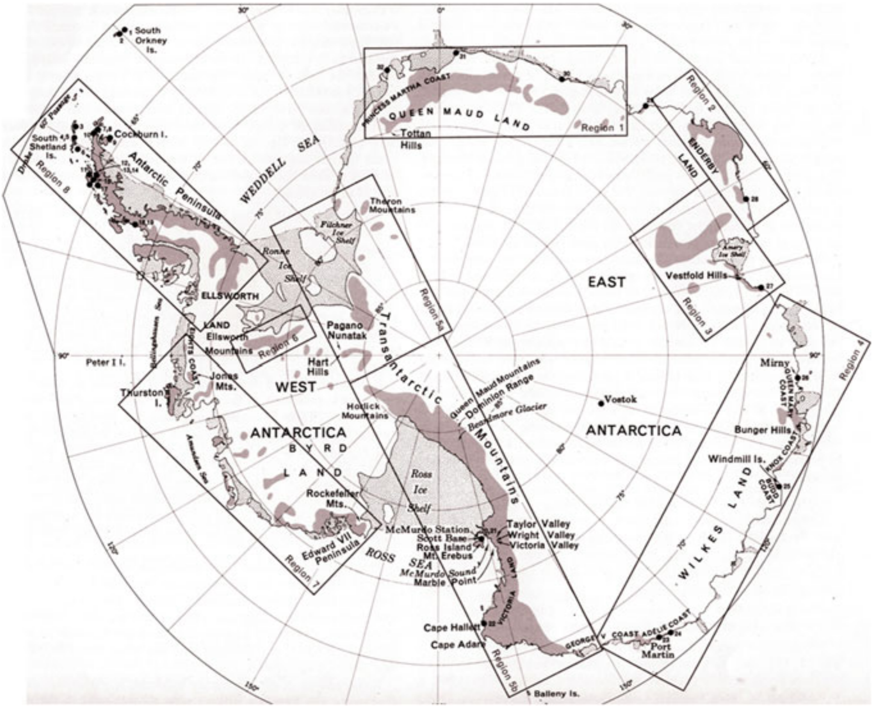

Fig. 16.1 Key ice-free areas of Antarctica and place names mentioned in this chapter (from Greene et al. 1967). The numbered soil regions correspond to those in Tables 16.1, 16.2, 16.4, 16.5, 16.6, 16.7

an unfrozen zone between the solum (soil profile) and the permafrost. In the very-cold-hyperarid-inland climate, the soils are developed less deeply and may contain "dry" permafrost above the ice-cemented layer. Permafrost is defined on the basis of temperature and not moisture content, which means, dry permafrost represents dry-frozen material that has formed from sublimation of ice in a hyperarid climate.

Time is an important soil-forming factor. Landforms in Antarctica range from late Holocene along the western Antarctic Peninsula and in coastal areas throughout Antarctica to Miocene (11–14 My) in the Transantarctic Mountains. Soils undergo a maturation process like other natural bodies. Time of exposure is the most important factor influencing functional diversity of soils in the Transantarctic Mountains, including depths of staining, coherence, visible salts, and ghosts (pseudomorphs of weathered clasts); depth of ice-cemented permafrost; maximum color-development equivalence; salt and weathering stages; thickness of the salt pan; salt concentration in the salt-enriched layer, and the profile salt content to 70 cm (Bockheim 2008).

Relief and parent materials are important, particularly in the South Shetland Islands, where geomorphic processes such as debris flows and active-layer detachment slides are particularly active (López-Martínez and Serrano 2002), and

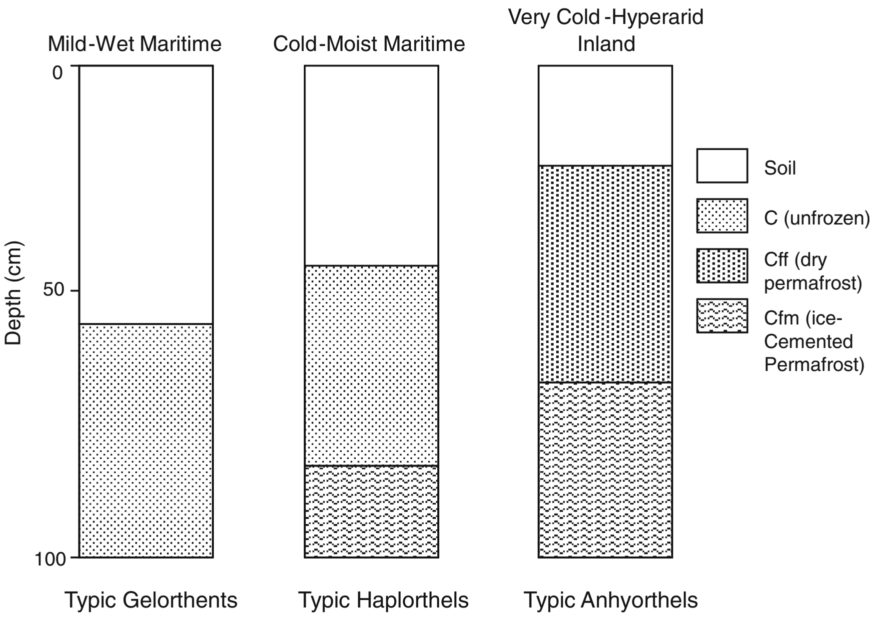

Fig. 16.2 Diagrammatic cross sections of soils representative of the three major climate regions of Antarctica

organisms are important in coastal areas where plants and animals are most abundant (Ugolini 1970).

There are at least nine soil-forming processes that operate at different magnitudes in ice-free areas of Antarctica (Fig. 16.3). Rubification, or reddening of the soil from oxidation of iron-bearing minerals, is a dominant process in maritime Antarctica (Fig. 16.4a). Similarly, carbonation, the formation of secondary carbonates, and humification, the buildup of organic matter on the surface and within the upper mineral soil (Fig. 16.4b), are key processes in maritime Antarctica, where moisture and plants are prevalent. Podzolization occurs to a limited extent in coastal Antarctica, primarily in abandoned penguin rookeries (Fig. 16.4c; Beyer and Bölter 2000). Phosphatization is the accumulation of phosphate minerals in soils of active penguin rookeries (Simas et al. 2007; Fig. 16.4d). This process is most pronounced in maritime Antarctica. Cryoturbation, or frost mixing, requires moisture and fluctuating soil temperature and commonly occurs in maritime Antarctica (Fig. 16.4e). In contrast, processes such as salinization and alkalization (i.e., the accumulation of sodium and calcium salts, Fig. 16.4f), desert pavement formation, and the formation of thick permafrost are dominant in the very-cold-hyperarid inland areas of Antarctica. The factors and processes of soil formation control the nature and properties of soils as well as their distribution.

This chapter addresses the following items: (1) background information on soil concept and the soil-forming factors and processes; (2) properties of Antarctic

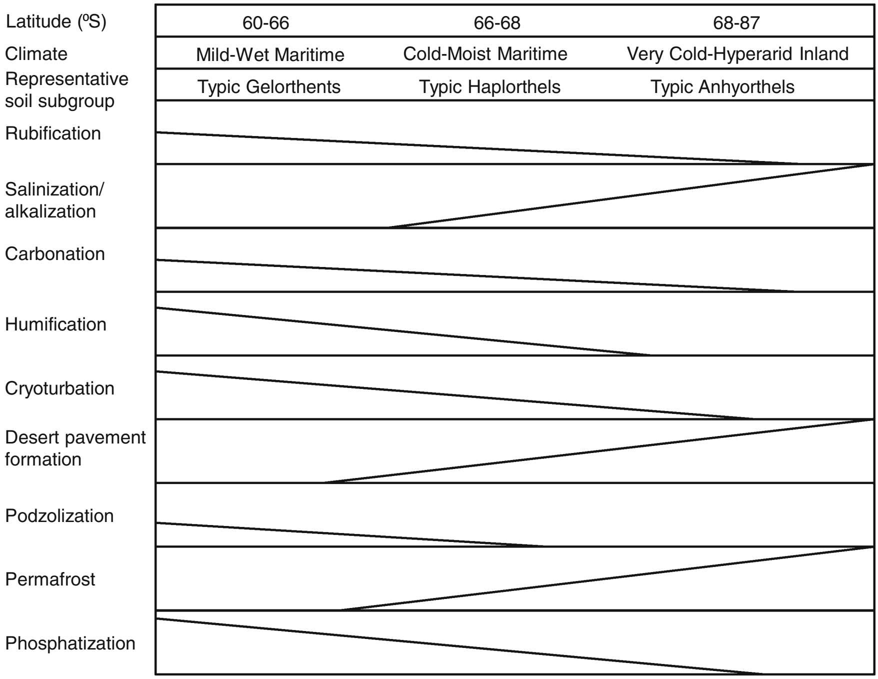

Fig. 16.3 Changes in pedogenic processes along a latitudinal climate gradient in Antarctica (revised from Bockheim and Ugolini 1990)

soils; (3) classification of Antarctic soils; and (4) soilscapes in Antarctica, particularly as they relate to the distribution of biota.

16.2 Properties of Antarctic Soils

16.2.1 Physical Properties

Soils of Antarctica are derived primarily from glacial deposits, colluvium (deposits moved downslope by gravity), residuum (material formed in situ), and alluvium, with lesser areas of glaciolacustrine, eolian, volcanic ash, and other materials. The nature of these materials influences the physical properties of Antarctic soils, such as soil texture, bulk density, soil-moisture regime, and soil-temperature regime. Most of the soils of Antarctica contain abundant coarse fragments (>2 mm); and the fine-earth fraction (<2 mm) usually is dominated by sand (2–0.05 mm; Table 16.2). In mineral soils, clay contents are generally low, ranging from 0 to 15 %. Similarly, silt contents often are low, especially in the inland mountains where low temperatures and hyperarid conditions reduce physical and chemical weathering.

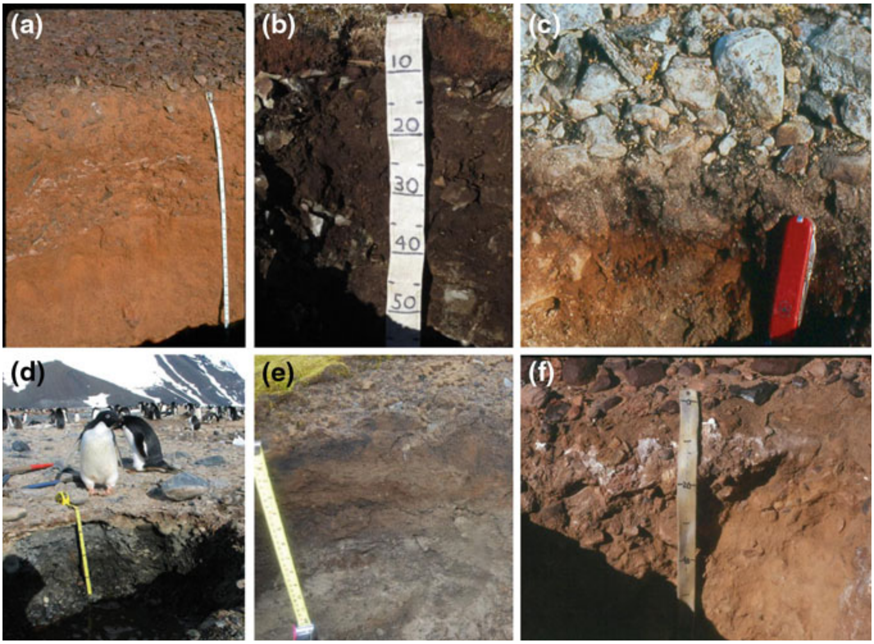

Fig. 16.4 Examples of specific soil-forming processes in soils of Antarctica. **a** A Miocene aged soil from Arena Valley showing rubification. **b** An umbric epipedon in a soil from the Antarctic Peninsula showing accumulation of organic carbon (humification) in the mineral soil. **c** A Typic Spodorthel from Casey Station (photograph by M. Bölter). **d** An ornithogenic soil from Cape Hallett (photograph by M. Balks). **e** Cryoturbation in a soil from Livingston Island, South Shetland Islands. **f** A salt pan in a soil from Mt. Fleming, McMurdo Dry Valleys

Bulk density is largely dependent on particle-size distribution and organic C concentration. In the MDVs, the soils are often sandy, contain less than 0.05 % soil organic carbon (SOC), and have bulk densities ranging between 1.5 and 1.7 g cm^{-3} (Table 16.2). However, in ornithogenic and organic soils, especially in Regions 4 and 8, bulk densities of 0.1–0.6 g cm^{-3} are common (Blume et al. 2002).

Campbell et al. (1997) determined the moisture content of 141 soils in the MDVs, reporting ranges of soil-moisture contents in the active-layer permafrost and near-surface permafrost of 0.2–12 and 1–15 %, respectively (Table 16.3). The range in gravimetric moisture contents varies strongly by microclimate zonation: Coastal Thaw Zone > Inland Mixed Zone > Stable Upland. The lower values for permafrost are for dry-frozen materials, and the higher values are for ice-cemented materials. According to their study, only 3 % moisture on a weight basis is required for cementation of the soil.

The concept of “anhydrous conditions” was developed in “soil taxonomy” (Soil Survey Staff 2010), especially for hyperarid soils of Antarctica. Anhydrous conditions refer to the moisture conditions in soils of cold deserts with dry

Table 16.1 Climate of ice-free areas in Antarctica[a] (regions are shown in Fig. 16.1)

No.	Region	Representative station	Latitude	Longitude	MAAT[b] (°C)	MAP[c] (mm)	Active-layer depth[d] (cm)	TTOP[e] (°C)
1	Drønning Maud Land	Sanae	70°19′S	2°21′W	−17.2		15–40	−16.8
2	Enderby Land	Molodezhnaya	67°40′S	45°50′E	−10.8	712	40–55	−9.8
3	Vestfold Hills	Davis	68°35S	77°58′E	−10.3	∼500	35–55	−8.5
4	Wilkes Land	Casey	66°17′S	110°32′E	−9.3	230	30–60	
5a	Pensacola Mountains	(None)	82°27′S	51°17′W	−25	150		
5b	Transantarctic Mountains	Vanda	77°31′S	161°40′E	−19.3	∼10	20–45	−17.3
6	Ellsworth Mountains	(None)	78°31′S	161°40′E	−24	250	15–50	
7	Queen Maud Land	Russkaya	74°46′S	161°40′E	−12	200	10	−10.4
8	Antarctic Peninsula	Palmer	64°46′S	161°40′E	−1.7	1,500	>500	−0.9
8	Antarctic Peninsula	Arctowski	62°10′S	58°28′W	−1.8	510	50–200	–0.35

[a] *Sources* Bockheim (1995), Vieira et al. (2010)

[b] Mean annual air temperature

[c] Mean annual precipitation

[d] Seasonal thaw layer

[e] Temperature at the top of permafrost

permafrost. These soils typically receive less than 50-mm water-equivalent precipitation per year and have a moisture content of less than 3 % by weight. Elevated levels of soil moisture in what is described as hyporheic zones (wetted hydrologic margins) are important for soil organisms (Barrett et al. 2009). Additional information on this topic is given in Chap. 2.

The soil-temperature regime likewise is important for weathering processes and biota. Whereas soils in the Transantarctic Mountains are hypergelic [the mean annual soil temperature (MAST) at 50 cm is −10 °C or lower], soils in coastal areas are pergelic (the MAST ranges from −4 to −10 °C), and soils along the western Antarctic Peninsula and in the South Shetland Islands and South Orkney Islands are subgelic (the MAST is +1 to −4 °C) (Soil Survey Staff 2010). These temperature differences are reflected in the thickness of the active layer and the temperature at the top of the permafrost (TTOP; Vieira et al. 2010). The active-layer depth, ranges from 50 to >500 cm along the Antarctic Peninsula, where permafrost is present (Table 16.1), from 40 to 60 cm in coastal East Antarctica, and from 10 to 45 cm in the inland mountains. The TTOP ranges from −1 to −2 °C along the western Antarctic Peninsula (Region 8), from −8 to −10 °C in coastal East Antarctica (Regions 2–4), and from −10 to −18 °C in the inland mountains (Regions 1, 5–7).

Table 16.2 Physical properties of selected surface soils in Antarctica (regions are shown in Fig. 16.1)

Soil region	Area	Latitude	Longitude	Depth (cm)	Moisture content (%)	Bulk density (g cm^{-3})	Gravel (>2 mm)	Sand (%)	Silt (%)	Clay (%)	References
Mineral soils											
1	Sør Rondane Mountains	72°00′S	25°00′E	0–20			71	87	9	4	Matsuoka (1995)
3	Davis	68°32′S	77°58′E	0–5	3.8		18	92	5	3	Line (1988)
4	Casey	66°17′S	110°32′E	1–5		1.4	17	54	42	4	Blume et al. (2002)
5a	Pensacola Mountains	83°15′S	51°00′W	0–2	0.75			70	30	0	Parker et al. (1982)
5b	Taylor Valley	77°37′S	163°00′E	1–9			57	89	6	5	Pastor and Bockheim (1980)
5b	Cape Hallett	72°20′S	170°05′E	0–5			56	91	9	0	Campbell and Claridge (1968)
5b	Wright Valley	77°10′S	161°50′E	0.5–9		1.5	56	94	6		Bockheim (1978)
5b	Victoria Valley	77°23′S	162°00′E	0–10	3.1	1.66		91	7	2	Cameron (1972)
5b	Marble Point	77°25′S	163°41′E	0–5	2.4						Aislabie et al. (2006)
5b	Mt. Fleming	77°33′S	160°17′E	1–5	4						Aislabie et al. (2006)
5b	Arena Valley	77°32′S	160°59′E	0–5			44	90	4	6	Bockheim (1997)
5b	Taylor Valley	77°43′S	162°22′E	0–10	4.8			93	2	5	Blecker et al. (2006)
5b	Asgard Range	77°36′S	161°05′E	0–40		1.63					McKay et al. (1998)
5b	Shackleton Glacier	85°00′S	175°00′W	0–5			56	89	9	2	Claridge and Campbell (1968)
5b	Beardmore Glacier	85°30′S	165°00′W	0–10				75	10	15	Bockheim et al. (1990)
8	Fildes Peninsula, King George Island	62°12′S	58°58′W	0–7			23	43	51	6	Chen and Blume (2000)
8	Fildes Peninsula, King George Island	62°37′S	61°06′W	0–5			45	58	33	9	Navas et al. (2008)
8	Palmer	64°46′S	64°04′W								Haus and Bockheim (unpublished)

(continued)

Table 16.2 (continued)

Soil region	Area	Latitude	Longitude	Depth (cm)	Moisture content (%)	Bulk density (g cm^{-3})	Gravel (>2 mm)	Sand (%)	Silt (%)	Clay (%)	References
8	Elephant Island	61°08′S	55°07′W	0–5				51	39	10	O'Brien et al. (1979)
8	Livingston Island	62°37′S	61°06′W	0–5				46	42	12	Navas et al. (2008)
8	Signy Island	60°43′S	45°38′W	0–10				90	6	4	Allen et al. (1967)
	Average Antarctic Peninsula						34	58	34	8	
	Average East Antarctica				3.8	1.40	18	73	24	4	
	Average Inland Mountains				3.0	1.60	54	87	9	4	
Ornithogenic soils											
8	King George Island	62°10′S	58°28′W	0–10				53	27	20	Michel et al. (2006)
8	King George Island	62°04′S	58°24′W	0–10			69	75	15	10	Simas et al. (2008)
8	King George Island	62°10′S	58°28′W	0–19		1.3	30	85	12	3	Blume et al. (2002)
8	Cierva Point	64°10′S	60°51′W	0–1	49						Mataloni et al. (2010)
	Average				49	1.3	49.5	71	18	11	
Organic soils											
4	Casey	66°17′S	110°31′E	4–15				40	41	19	Beyer and Bölter (2000)
8	King George Island	62°12′S	58°58′W	0–7			55	34	55	11	Chen and Blume (2000)

Table 16.3 Gravimetric moisture content of the active-layer permafrost and near-surface permafrost of selected locations in the McMurdo Dry Valleys (Campbell et al. 1997)

Location	No. of sites	Moisture (%)	
		Active layer	Permafrost
Coastal thaw zone[a]			
Marble Point	13	1.9–9.5	3–15
Scott Base	37	3.4–12	4–10
Cape Evans	3	4.6	–
Cape Roberts	3	0.2–10.8	–
Inland mixed zone			
Vanda	53	0.5–4.3	1
Dias	1	1.8	1
Barwick Valley	1	6.9	–
Greenville Valley	6	0.6–6.7	3
Stable upland			
Asgard Range	1	1.4	–
Beacon Heights	13	0.3–2.8	1–14
Mt. Brooke	10	0.4–4.5	1–2

[a] Microclimate zonation (Marchant and Head 2007)

16.2.2 Chemical Properties

Key chemical properties of Antarctic soils which are related to the distribution and abundance of soil organisms include pH; organic and inorganic C and N concentrations; extractable, organic or total P; and the concentration of soluble salts. Soil climate plays an important role in all of these properties. In the surface mineral soil, soil organic carbon (SOC) concentrations average 2.0, 0.9, and 0.1 % in soils of the western Antarctic Peninsula, coastal East Antarctica, and the inland mountains, respectively (Table 16.4). Ornithogenic and organic soils contain much higher levels of SOC, averaging 13.6 and 59 %, respectively. With the climate warming along the western Antarctic Peninsula, there is considerable current interest in levels of soil inorganic carbon (SIC) and soil organic carbon (SOC) in Antarctic soils. The SOC in Antarctic soils is important as a source of energy and nutrients to microorganisms and other soil biota (Powers et al. 1998; Courtright et al. 2001; Zeglin et al. 2009).

Beilke and Bockheim (2013) measured organic and inorganic forms of C and N in five soil chronosequences in the Transantarctic Mountains. Carbon levels decreased with drift age for two of the sequences, due primarily to high levels of C in young ice-cored drifts. Carbon increased with drift age for the Beardmore Glacier sequence due to the presence of coal in older drifts. Nitrogen increased with drift age for a majority of the soil chronosequences. Inorganic C and all forms of N were significantly and positively correlated with mean annual precipitation. Their results suggested that C levels in similar settings do not significantly change

Table 16.4 Chemical properties of selected surface soils in Antarctica (regions are shown in Fig. 16.1)

Soil region	Area	Latitude	Longitude	Depth (cm)	pH	EC (dS m^{-1})	SOC (%)	P^a (mg kg^{-1})	References
Mineral soils									
2	Molodezhnaya	67°40′S	45°51′E	0–5	5.8		0.46	1,100 (o)	Negoita et al. (2001)
3	Davis	68°32′S	77°58′E	0–5	6.3	0.9			Line (1988)
4	Casey	66°17′S	110°32′E	0–5	4.5	2.3	1.4	z	Blume et al. (2002)
5a	Pensacola Mountains	83°15′S	51°00′W	0–3	6.5	9.5		0.40 (e)	Cameron and Ford (1974)
5b	Taylor Valley	77°37′S	163°00′E	0–9	7.4	6.8			Pastor and Bockheim (1980)
5b	Cape Hallett	72°20′	170°05′E	0–5	9.6				Campbell and Claridge (1968)
5b	Wright Valley	77°10′S	161°50′E	0.5–9	6.8	9.6			Bockheim (1978)
5b	Victoria Valley	77°23′S	162°00′E	0–10	6.8	3	0.05	0.26 (e)	Cameron (1972)
5b	Marble Point	77°25′S	163°41′E	0–5	9.6	0.65	0.28		Aislabie et al. (2006)
5b	Mt. Fleming	77°33′S	160°17′E	0–5	6.2	4.4	0.01		Aislabie et al. (2006)
5b	Shackleton Glacier	85°00′S	175°00′W	0–5	6.5				Claridge and Campbell (1968)
5b	Beardmore Glacier	85°30′S	165°00′W	0–5		2.9			Bockheim et al. (1990)
5b	Arena Valley	77°32′S	160°59′E	0–5	6.2	4			Bockheim (1997)
5b	Taylor Valley	77°43′S	162°22′E	0–10	8.5		0.16		Blecker et al. (2006)
5b	Bull Pass	77°31′S	161°52′S	0–2	7.6	5.6	0.03		Aislabie et al. (2006)
5b	Vanda	77°31′S	161°40′S	0–2	9.1	0.09	0.06		Aislabie et al. (2006)
6	Edson Hills, Ellsworth Mountains	79°50′S	83°39′W	0.5–7	7.7	1.7			Denton et al. (1992)
8	Byers Peninsula, Livingston	62°37′S	61°06′W	0–5	4.6	0.12	0.29	10 (e)	Navas et al. (2008)
8	Palmer	64°46′S	64°04′W						Haus and Bockheim (unpublished)
8	Signy Island	60°43′S	45°38′W	0–10	5.4		6.9	50 (e)	Allen et al. (1967)
8	Elephant Island	61°08′S	55°07′W	0–5	8.2	0.19	0.33	2,200 (?)	O’Brien et al. (1979)

(continued)

Table 16.4 (continued)

Soil region	Area	Latitude	Longitude	Depth (cm)	pH	EC (dS m^{-1})	SOC (%)	P^a (mg kg^{-1})	References
8	Livingston Island	62°37′S	61°06′W	0–5	7.2	0.1	0.6	7 (e)	Navas et al. (2008)
	Average Antarctic Peninsula				6.4	0.1	2		
	Average East Antarctic				5.5	1.6	0.9		
	Average Inner mountains				7.6	4.4	0.1		
Ornithogenic soils									
5a	Cape Royds	77°33′S	166°09′E	0–3			21.8	z	Ugolini (1972)
8	King George Island	62°10′S	58°28′W	0–10	5		8.6	622 (m)	Michel et al. (2006)
8	King George Island	62°04′S	58°24′W	0–10	5.9		32		Simas et al. (2006)
8	King George Island	62°10′S	58°28′W	0–19	4.2	0.3	8	z	Blume et al. (2002)
8	Cierva Point	64°10′S	60°51′W	0–1	4.1	0.26	8.4	451 (e)	Mataloni et al. (2010)
8	King George Island	62°12′S	58°58′W	0–4	4.9		11		Chen and Blume (2000)
	Average				4.8	0.3	13.6		
Organic soils									
4	Casey	66°17′S	110°32′E	4–15	4	1.3	133	21 (o)	Beyer and Bölter (2000)
8	King George Island	62°12′S	58°58′W	0–7	5.1		14.3		Chen and Blume (2000)
8	Argentine Islands	65°20′S	64°08′W	0–4	3.9		29.6	0.38 (t)	Parnikoza et al. (2011)
	Average				4.3	1.3	59		

[a] P form: *o* organic; *e* extractable (water); *m* extractable (Mehlich); *t* total; *?* unknown

over time and that changes in temperature or moisture associated with microclimate likely play a much larger role in C and N levels.

Inorganic C has been studied in the MDVs. Although stages I and II (encrustations below stone and flecks, respectively) carbonates occur in these soils, calcic and petrocalcic horizons are uncommon. Foley et al. (2006) reported that pedogenic carbonates in till of Taylor Valley originated primarily from old lakes along the valley floor and that carbonate concentrations were very low above these ancient lakes.

The reaction of surface mineral soils in Antarctica is usually slightly acid to slightly alkaline (pH 6.4–7.6; Table 16.4). Soils derived from calcareous materials, such as at Marble Point and Cape Hallett, are highly alkaline (pH 9.6). Ornithogenic and organic soils generally are highly acidic (pH 3.9–5.1) due to elevated concentrations of ammonium and organic acids, respectively.

Whereas soils of Antarctic Peninsula and coastal East Antarctica (Regions 2–4, 8) occur in a leaching environment and are nonsaline [electrical conductivity (EC) < 2 dS m^{-1}], soils of the inland mountains often are saline (EC > 4 dS m^{-1}; Table 16.4). Electrical conductivity values as high as 85 dS m^{-1} have been reported in Pliocene-aged Alpine IV moraines in Wright Valley (Bockheim and McLeod 2006). In the MDVs, salts in soils are determined by marine aerosols (Claridge and Campbell 1977) and are dependent on proximity to the coast (Bockheim 1997). Whereas NaCl is common in salic and petrosalic soils along the McMurdo coasts, gypsic and petrogypsic soils may occur further inland; and soils along the polar plateau are influenced by $NaNO_3$ and contain nitric and petronitic[1] horizons (Bockheim 1997). These trends are reflected by soil minerals as well as the dominant cations and anions in 1:5 soil–water extracts. High levels of salts are detrimental to many soil organisms (Powers et al. 1998; Courtright et al. 2001; Poage et al. 2008; Zeglin et al. 2009; Aislabie et al. 2011).

The level of P in Antarctic soils is controlled almost entirely by the influence of birds and mammals (Table 16.4). Phosphatization is a dominant soil-forming process in these soils as evidenced by the existence of struvite and other secondary phosphate minerals and high levels of extractable P (Simas et al. 2007). Phosphorus is a critical element and is limiting for lysogenic bacteria in the MDVs (Lisle and Priscu 2004).

16.2.3 Chemical Weathering and Mineral Alteration

There is a common notion that chemical weathering and mineral alteration must be minimal in Antarctica. However, mineral transformations are common along the Antarctic Peninsula and in the inland mountains. In the McMurdo Dry Valleys, common mineral transformations in the clay (<2 μm) fraction are alteration of feldspars to mica, mica to smectite, and vermiculite to interstratified vermiculite–smectite (Table 16.5). Zeolites (chabazite, phillipsite) are commonly found in soils of the MDVs (Linkletter 1974; Gibson et al. 1983; Claridge and Campbell 2008).

Weathering occurs in thin hulls of unfrozen water held at high tensions (Ugolini and Jackson 1982).

At least four weathering reactions have been identified in the South Shetland Islands: (1) alteration of feldspars to smectite, kaolinite, and zeolites (e.g., laumonite); (2) weathering of smectite to hydroxy-interlayer smectite and allophone; (3) production of leucophosphate from penguin guano; and (4) the formation of jarosite in acid-sulfate soils (Simas et al. 2006; Navas et al. 2008; Table 16.5).

16.3 The Classification of Soils in Antarctica

There are two general kinds of soil classification systems used in Antarctica: "genetic" systems and "natural" systems. Genetic systems are based on presumed pedogenic processes and can only be applied broadly to Antarctica. Natural systems classify soils based on their properties and often use a hierarchical approach. An example of a genetic system is that of Tedrow (1966) who divided "soils of the cold desert" into (1) ahumic soils; (2) evaporite soils; (3) protoranker soils; (4) ornithogenic soils; (5) regosols; and (6) lithosols (rockland). Campbell and Claridge (1987) expanded upon this approach and classified "frigic" soils of Antarctica into zonal, intrazonal, and azonal groups. Zonal soils are assumed to be controlled dominantly by climate and were subdivided into subgroups based on available moisture status (ultraxerous, xerous, and subxerous), degree of soil development (weakly, moderately, and strongly developed), and parent material (origin and composition). Intrazonal soils included all those in groups 2 through 4 in the Tedrow and Ugolini (1966) classification, and azonal soils included those in group 5, i.e., soils of recent beaches, fans, and stream beds.

"Soil taxonomy" (Soil Survey Staff 2010) is an example of a natural system that employs soil properties in diagnostic surface (epipedons) and subsurface horizons in a hierarchical manner to classify soils. There are 12 orders in "soil taxonomy" (ST), four of which occur in Antarctica. Three of the orders occur in areas lacking permafrost or where permafrost is deeper than 1 or 2. These include the Histosols (organic soils), Inceptisols (weakly developed soils), and Entisols (very weakly developed soils, i.e., "recent" soils). The dominant soil order in Antarctica is the Gelisols, the permafrost-affected soils. Gelisols are divided into three suborders: those derived from organic materials (Histels), mineral soils with cryoturbation (frost-sorting; Turbels), and mineral soils with permafrost within 1 m of the surface but with minimal cryoturbation (Orthels). These suborders are divided into great groups based on other key characteristics, subgroups based on their linkage with other soils, and families based on properties important to organisms (e.g., soil temperature, soil moisture, mineralogy, soil reaction class, etc.). In the discussion that follows, ST will be used to discuss soil patterns in Antarctica.

Table 16.5 Chemical weathering and mineralogical changes in the clay fraction (<2 μm) of soils in Antarctica (regions are shown in Fig. 16.1)

Soil region	Area	Latitude	Longitude	Mineral transformation	References
5b	Wright Valley	77°30′S	161°52′E	Feldspar > mica Vermiculite > vermiculite-smectite	Ugolini and Jackson (1982)
5b	Taylor Valley	77°37′S	163°00′E	Vitric ash > phillipsite	Linkletter (1974)
5b	Taylor Valley	77°37′S	163°00′E	Mica > hydrated mica	Claridge (1965), Pastor and Bockheim (1980)
5b	Marble Point	77°27′S		Biotite > limonite	Kelly and Zumberge (1961)
5b	Cape Hallett	72°20′S	170°05′E	Hydrous mica > smectite	Campbell and Claridge (1968)
5b				Chlorite > vermiculite Mica > vermiculite	Claridge (1965)
5b	Brown Hills	79°52′S	165°10′E	Ferromagnesian > smectite	Claridge and Campbell (1984)
5b	Wright Valley	77°30′S	161°52′E	Plagioclase > zeolites (chabazite)	Gibson et al. (1983)
8	King George Island	62°04′S	58°24′W	Smectite > hydroxy-interlayer smectite, allophane Penguin guano > leucophosphate Sulfides > jarosite Plagioclase > kaolinite	Simas et al. (2006)
8	Livingston Island	62°37′S	61°06′W	Orthoclase feldspar > smectite Plagioclase > zeolites (laumonite)	Navas et al. (2008)

16.4 Soilscapes of Antarctica

Soil patterns, or soilscapes, in Antarctica may be as complex as in other ecoregions of the world. Soil maps have been prepared at a reconnaissance scale for the Transantarctic Mountains, the Ellsworth Mountains, and valleys within the McMurdo Dry Valleys system. Detailed maps are available for Seabee Hook at Cape Hallett (Region 5b), Casey station (Region 4), and the Byers Peninsula of King George Island (Region 8; Table 16.6). This table indicates that about 53 % (26,375 km^2) of the ice-free area of Antarctica has been mapped; however, the most of the mapped area is in the Transantarctic Mountains at a scale of 1:1 million.

Permafrost is lacking in the upper 2 m of the mild-wet maritime sector of the western Antarctic Peninsula. Soils in this region are primarily Entisols, Inceptisols, and Histosols, with Typic Gelorthents and Typic Gelaquents being most common (Table 16.7). The abundance of underground streams and cryoturbation in this region also lead to the formation of Turbic Dystrogelepts and Turbic Humigelepts. Some of the organic soils are comprised of highly decomposed materials and are classified as Saprists. The South Shetland Islands contain a diversity of soils, including Orthels (Moll-, Umbr-, Psamm-, Hapl-), Turbels (Aqui-, Umbri-, Haplo-), and Sapristels, as well as Entisols, Inceptisols, and Histosol-lacking permafrost (Blume et al. 2002).

In coastal East Antarctica, permafrost is common in the upper 1 m, and the soils are dominantly Haplorthels and Aquiturbels. However, Lithic and Typic Spodorthels occur in abandoned penguin colonies from podzolization. The inland mountains contain permafrost within 0.2–0.5 m of the surface, anhydrous conditions, and feature Lithic and Typic Anhyorthels and Anhyturbels as well as Lithic and Typic Haplorthels and Haploturbels (Table 16.7).

Water is the limiting factor controlling the distribution and diversity of organisms in continental Antarctica, including cryptogams and microarthropods (Kennedy 1993), nematodes (Powers et al. 1998; Courtright et al. 2001), and microorganisms (Bamforth et al. 2005). More specifically, microbial and soil invertebrate abundance are strongly related to vegetation and vegetation-associated soil properties (e.g., water content, organic C, total N) (Powers et al. 1998). There is often a negative correlation with the number of soil invertebrates and soil salinity (Powers et al. 1998; Courtright et al. 2001; Poage et al. 2008; Aislabie et al. 2011). These points are summarized in Table 16.8, which identify ecologic factors important for life in Antarctica.

Based on these relations, the preferred soil taxa for soil organisms would be Inceptisols (Typic Dystrocryepts, Typic Humigelepts), Entisols (Typic Gelaquents), and Histosols (Typic Cryosaprists) in areas lacking or containing permafrost below 1–2 m. In areas with permafrost-affected soils, taxa with abundant soil moisture would be the most favorable habitats, including Typic Haploturbels, Typic Haplorthels, Typic Aquiturbels, Typic Aquorthels, Glacic Haploturbels,

Table 16.6 Soil maps available for Antarctica (regions are shown in Fig. 16.1)

Region	Area	Approximate scale	Ice-free area mapped (km^2)	Number of subgroups	References
4	Casey Station, Windmill Island	1:2,000	0.04	5	Beyer and Bölter (2000)
5a	Pensacola Mountains	1:500,000	1,500	6	Bockheim and McLeod (unpublished)
5b	Taylor Valley	1:250,000	545	7	Bockheim et al. (2008)
5b	Wright Valley	1:50,000	495	13	McLeod et al. (2008)
5b	Arena Valley	1:50,000	68	13	Bockheim (2007)
5b	Beacon Valley	1:50,000	215	3	Bockheim (2007)
5b	Royal Society Range	1:50,000	560	3	Bockheim (unpublished)
5b	Seabee Hook, Hallett	1:2,000	0.23	3	Hofstee et al. (2006)
5b	Transantarctic Mountains	1:1,000,000	24,200	10	Bockheim et al. (2007)
6	Ellsworth Mountains	1:500,000	2,100	2	Bockheim (unpublished)
7	Russkaya Station, M. Byrd Land	1:1,000	1.7	6	Lupachev et al. (unpublished)
8	Fildes Peninsula, King George Island	1:35,000	26	25	Schaefer et al. (unpublished)
8	Deception Island	1:50,000	47	10	Haus et al. (unpublished)
		Total	26,375		

Table 16.7 Dominant soil taxa by region in Antarctica (regions are shown in Fig. 16.1)

Region	Area	Dominant soil taxa[a]	References
1	Sør Rondane Mountains	TAo, THt > TAt > LHt	Matsuoka (1995)
2			
3			
4	Casey, Windmill Islands	THo, LHo > LSo, TSo > TAqt	Beyer and Bölter (2000)
5a	Pensacola Mountains		
5b	North Victoria (Cape Hallett)	THo > TAqo, THt	Hofstee et al. (2006)
5b	McMurdo Dry Valleys	TAo, THt > TAt > LHt > GHt, LAt	Bockheim and McLeod (2008)
5b	Darwin–Hatherton Glaciers	TAt > THt, LAt, TAo > LHt > GHt	Bockheim and McLeod (unpublished)
5b	Beardmore Glacier	TAo, LAt, TAt > THt, LHt	Bockheim and McLeod (unpublished)
5b	Shackleton Glacier	TAo > TAt > LAt, GHt, THt, LHt	Bockheim and McLeod (unpublished)
5b	Scott–Reedy Glaciers	TAt > THt > LAt, LHt, TAo	Bockheim and McLeod (unpublished)
6	Ellsworth Mountains	LHt > TAo > THo	Bockheim (unpublished)
7	Marie Byrd Land	LAo, LAt > AHo, AHt > LHo, LFs	Lupachev et al. (unpublished)
8	South Orkney Islands	LFs > TUt > Taqt, THt	Allen et al. (1967)
8	South Shetland Islands	THt, LHo > THo, FSs, CUt, TUo, TPo	Blume et al. (2002)
8	Western Antarctic Peninsula	TGe > TGq > TDp, THp, LHp, TCs	Haus and Bockheim (unpublished)

[a] *TAo* Typic Anhyorthels; *THt* Typic Haploturbels; *LHt* Lithic Haploturbels
THo Typic Haplorthels; *LHo* Lithic Haplorthels, *LSo* Lithic Spodorthels
TSo Typic Spodothels; *TAqt* Typic Aquiturbels; *TAqo* Typic Aquorthels
TAt Typic Anhyturbels; *GHt* Glacic Haploturbels; *LAt* Lithic Anhyturbels
LAo Lithic Anhyorthels; *AHo* Aquic Haplorthels; *AHt* Aquic Haploturbels
LFs Lithic Fibristels; *TUt* Typic Umbriturbels; *Cut* Cumulic Umbriturbels
TUo Typic Umbrorthels; *TPo* Typic Psammorthels; *FSs* Fluventic Sapristels
TGe Typic Gelorthents; *TGq* Typic Gelaquents; *TDp* Typic Dystrocryepts
THp Typic Humigelepts; *LHp* Lithic Humigelepts; *TCs* Typic Cryosaprists

Table 16.8 Ecologic factors favoring biota in Antarctica

Ecologic factor	Microorganisms	Microarthropods[a]	Macroarthropods[b]	Algae, cryptogams	Vascular plants
Site factor					
N–S orientation	x			x	
High solar radiation	x			x	
Protected habitat	x				
Absence of wind	x				
Low elevation		x		x	
Proximity to lakes, streams		x			
High humidities	x				
Slow or impeded drainage	x			x	
Translucent coarse fragments	x				
Soil factor					
Lengthy duration of available water content	x	x		x	x
Lengthy duration of soil temperature >0 °C	x			x	x
Nonsaline soils (Low EC)	x	x	x		x
Near-neutral pH	x	x	x		
Low inorganic N	x	x			
Abundant organic N	x		x		
Narrow C:N	x				
Abundant organic matter	x	x			

[a] Nematodes

[b] Tartigrades, rotifers, springtails (Collembola), mites (Acari)

Sources Cameron (1971), Powers et al. (1998), Courtright et al. (2001), Zeglin et al. (2009), Simmons et al. (2009), Ganzert et al. (2011), Lee et al. (2012)

Aquic Haplorthels, Aquic Haploturbels, Typic Umbriturbels, Cumulic Umbriturbels, Typic Umbrorthels, and Fluventic Sapristels.

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Chapter 17
Origins of Antarctic Soils

Bryan C. Storey

Abstract Antarctica has a long geological history that dates back to some of the oldest rocks known on planet Earth. The continent is divided physiographically by the high Transantarctic Mountains into the old East Antarctic basement domain with rocks up to 3.9 billion years old and a younger West Antarctic domain where rocks are mostly less than 500 million years old. Today, the continent is sitting largely within the Antarctic plate where it is covered by large ice sheets. The geological evolution of Antarctica including its subsequent glacial history, which is reviewed in this chapter, has been an important contributor to the formation of Antarctic soils in ice free regions.

17.1 Introduction

Although Antarctica is for the most part covered in ice, we have a clear understanding of its regional geology based on many years of geological investigations including outcrop mapping, aeromagnetic, gravity and radar surveys, seismic studies and geological drilling (Tingey 1991; Gamble et al. 2002). The continent is divided physiographically by the Trans-Antarctic Mountains, one of the Earth's major mountain ranges. The Trans-Antarctic Mountains represent an ancient suture (Stump 1995) that was reactivated during the final stages of the disintegration of Gondwana to form the present-day mountain range by crustal extension and uplift (Behrendt et al. 1991). The mountains extend for some 3,500 km across the continent between the Ross and Weddell seas, which are typically 100–200 km wide and reach elevations locally in excess of 4,500 m. This spectacular topographic feature defines a fundamental lithospheric boundary that has profound

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crustal anisotropy due to repeated cycles of tectonism and marks a boundary between two regions with quite different geological histories known as East and West Antarctica. East Antarctica, which is the old crystalline core (East Antarctic Shield) of ancient Gondwana and earlier supercontinents (Fitzsimons 2000), contains the oldest known rock in Antarctica and is largely covered by the 4-km-thick East Antarctic ice sheet. With the exception of the central Gamburtsev Mountains, a high subglacial mountain range of unknown origin, East Antarctica has a subdued topography. West Antarctica, on the other hand, is made up of much younger rocks, mostly less than 500 million years old. It has horst and graben topography with the spectacular Ellsworth Mountains hosting the highest mountain in Antarctica, Mt Vinson. A high Andean mountain chain occupies the spine of the Antarctic Peninsula.

For the past 35 million years or so, Antarctica has been isolated in a south polar position and for the most part covered in ice (Barrett 1999). During that time period, although ice has been permanent on Antarctica, ice has advanced and retreated many times as global climatic conditions have fluctuated.

Today, Antarctica is isolated in a south polar position sitting within a large Antarctic plate. With the exception of one small segment of the Antarctic Peninsula and Scotia Arc, the Antarctic plate is completely surrounded by spreading ridges (Torsvik et al. 2008). Consequently, the continent has low seismicity and few active volcanoes.

17.2 The East Antarctic Shield

The East Antarctic Shield comprises a Precambrian to Ordovician basement of igneous and sedimentary rocks deformed and metamorphosed to varying degrees and intruded by syn- to post-tectonic granites (Fitzsimons 2000). This basement is locally overlain by undeformed Devonian to Jurassic sediments (Beacon Supergroup) and intruded by Jurassic tholeiitic plutonic and volcanic rocks. Although much of the East Antarctic Shield is covered by the thick East Antarctic ice sheet, the application of traditional and modern U–Pb zircon and other dating techniques has shown that the shield has a three-stage tectonic history details of which are only just becoming evident (Fitzsimons 2000). These involve

1. The stabilization of various Archean to Palaeoproterozoic cratons (3.0 to 1.6 Ga). These areas of ancient crust can be divided into an extensive central craton, the Mawson continent inferred to occupy much of the continental interior of the East Antarctic Shield and various marginal cratons exposed along the coast. The marginal Archean cratons are correlated with similar cratons that rifted from Antarctica during the Mesozoic break-up of Gondwana, for example the Kaapvaal-Zimbabwe Craton of southern Africa, and the Dharwar Craton of southern India. One of these, the Napier Complex contains the oldest rock, dated at 3930 ± 10 Ma, currently known from Antarctica.

Fig. 17.1 Granite gneisses at Haag Nunataks, typical of metamorphic basement rocks found extensively within East Antarctica

2. The development of three high-grade Late Mesoproterozoic to Early Neoproterozoic mobile belts. These were previously assumed to form one single Grenville-age orogen around the coastline of East Antarctica but now appear to represent distinct crustal fragments juxtaposed in the Cambrian. One of these belts (Fig. 17.1), according to the SWEAT hypothesis, was used as a piercing point linking North America and East Antarctica in the Rodinia supercontinent between 1100 and 750 Ma (Moores 1991; Dalziel 1992).
3. Two Late Neoproterozoic to Cambrian 'Pan-African' mobile belts which rework, truncate and offset the above mobile belts, indicating that the East Antarctic segment of Gondwana underwent significant reorganization during the assembly of Gondwana at the Precambrian–Cambrian boundary. One of these belts is a continuation of the East African orogen and developed during closure of the Mozambique Ocean and the ultimate amalgamation of Gondwana. It is unclear the extend to which the other belt involved ocean closure or regional scale transcurrent tectonics.

It is not known whether the centre of the East Antarctic Shield is a single Palaeoproterozoic craton (Mawson continent), as commonly assumed, or whether it is cut by Grenville-age or Pan-African mobile belts, which would require modification of the boundaries of the Mawson continent. This uncertainty means that the various terranes exposed on the coast can be joined in any number of ways, and it follows that current models for Phanerozoic tectonics in East Antarctica and for global tectonics, given the crucial location of Antarctica in proposed supercontinents, will remain poorly constrained until some understanding of the continental structure beneath the ice cap is achieved.

17.3 The Trans-Antarctic Mountains

Marking the boundary between East and West Antarctica, the present-day intracratonic mountain chain has undergone episodic uplift since the Early Cretaceous and has been modelled as a major rift shoulder. The unifying geological feature of the mountains is a Middle Palaeozoic erosion surface (Kukri Peneplain) that separates gently tilted Devonian to Triassic sedimentary rocks (Gondwana cover sequence) and Jurassic continental tholeiites (Ferrar Supergroup) from a Proterozoic to Early Palaeozoic orogenic belt known as the Ross Orogen (Stump 1995) .

17.3.1 The Ross Orogen: The Palaeo-Pacific Margin of Gondwana

The SWEAT hypothesis linking the North American Laurentian continent with East Antarctica has provided a powerful tectonic framework for interpreting the Late Proterozoic and Early Palaeozoic siliciclastic turbidites and volcanic rocks exposed along the Trans-Antarctic Mountains as being deposited in a rift margin setting following the separation of Laurentia from Antarctica circa 750 Ma (Dalziel 1992). Following a folding event, known as Beardmore folding, carbonates were deposited along the margin in Early Cambrian times. Outboard of the Early Cambrian limestone, Middle Cambrian carbonates, sedimentary rocks and a bimodal volcanic sequence formed. The margin was subsequently transformed to an active Early Palaeozoic orogenic setting following the initiation of subduction of newly created proto-Pacific oceanic lithosphere beneath the rifted margin. Active deformation, volcanism, metamorphism and emplacement of subduction-related igneous rocks known as the Granite Harbour Intrusives occurred along the mountain front from circa 520 to 480 Ma. Large volumes of molasses sediment were shed to forearc marginal basins in Middle Cambrian and Ordovician time primarily by erosion of volcanic rocks of the Early Ross magmatic arc. The forearc deposits were intruded by late orogenic plutons as the locus of magmatism shifted offshore. Deposition of individual molasse sequences continued until 490 to 485 Ma. Three exotic terranes were emplaced along the North Victoria Land margin during the late stage of the Ross Orogeny.

Fig. 17.2 Dolerite sills of Jurassic age emplaced within sedimentary rocks of the Beacon Supergroup in the McMurdo Dry Valleys

17.3.2 Gondwana Cover Sequences: A Stable Continent

Unconformably overlying the deformed basement rocks of the Ross Orogen in the Trans-Antarctic Mountains and in the once neighbouring Gondwana continents is a flat lying cover sequence as much as 2.5 km thick known in Antarctica as the Beacon Supergroup (Barrett 1991). It represents a period of tectonic stability within the Gondwana continent that spans the Devonian to the Triassic. It is capped by basalt flows and intruded by thick dolerite dykes and sills of Middle Jurassic age (circa 180 Ma), a large igneous province known as the Ferrar province that heralded the break-up of Gondwana (Fig. 17.2).

There are four phases of sedimentation within the Beacon Supergroup and its scattered equivalents around the periphery of the East Antarctic Shield.

1. Devonian strata. The strata, which were deposited on an extensive undulating surface known as the Kukri Peneplain, are largely mature quartzose sandstones with red and green siltstones deposited by a mix of shallow marine and alluvial sedimentation during warm and semi-arid climatic conditions. Some of the strata contain fossil fish and characteristic trace fossils.
2. Permo-Carboniferous glacial deposits. In Late Carboniferous times, a thick ice sheet covered a large part of Gondwana including Antarctica, depositing a thick diamictite unit. The diamictite was deposited from a continental ice sheet and records at least four advances and retreat cycles ranging from 5 to 50 m thick. A thick glacial section in the northern part of the Ellsworth Mountains is

considered to be glacial marine in origin. Glacial striae and associated features have been measured and provide a relatively simple picture of ice flow away from the central Trans-Antarctic Mountains.

3. Permian sediments, the most widely distributed Beacon strata, are cross-bedded fine- to medium-grained sandstones, shale, and coal, the products of meandering braided rivers. Coal beds average about 1 m but range up to 10 m thick. The finer overbank deposits commonly contain the famous Glossopteris leaves, and fossilized stems and roots of the now extinct Glossopteris tree. The rapid and virtually complete disappearance of Late Palaeozoic ice is recorded in the earliest Permian strata. The Glossopteris leaves, dropped from the widespread woody deciduous tree or shrub, indicate a cool and wet rather than cold climate.
4. Following the end-Permian extinction event and the disappearance of the Glossopteris flora, the Triassic cross-bedded sandstones and mudstones were deposited by low sinuosity rivers on a north-west sloping plain. The reversal in palaeoslope is attributed to uplift associated with a Late Permian–Early Triassic Gondwanian folding, which deformed the Cape Fold Belt and also the Permian and older strata of the Ellsworth and Pensacola mountains in Antarctica. The climate was mild and arid with a varied reptilian and amphibian fauna, and a flora characterized by the fossil fern is known as Dicroidium.

Beacon sedimentation culminated in the Early Jurassic with explosive rhyolitic volcanism and volcanic debris flows and ultimately by Basaltic flows and associated intrusive rocks of the Ferrar Supergroup.

17.4 West Antarctica: A Collage of Crustal Blocks

The basin and range topography of West Antarctica can be used to delineate five physiographically defined crustal blocks that have distinctive geologically features and that may have existed as distinct microplates during the Mesozoic break-up of Gondwana (Dalziel and Elliott 1982; Storey 1996).

17.4.1 Haag Nunataks: Part of the East Antarctic Shield

This small crustal block is situated between the southern tip of the Antarctic Peninsula and the Ellsworth Mountains. It is formed entirely of Proterozoic basement amphibolites and orthogneiss with Grenvillian ages between 1176 and 1003 Ma (Fig. 17.1). Although the gneisses are only exposed on three small nunataks, aeromagnetic surveys show the full extent of the block and suggest that similar Proterozoic basement may underlie part of the Weddell Sea embayment region. Isotopic studies also suggest that it may be present beneath the neighbouring Antarctic Peninsula region. The gneisses correlate with Proterozoic basement gneisses within the East Antarctic Shield and may represent a fragment of the East Antarctic Shield displaced during the break-up of Gondwana.

17.4.2 Ellsworth Whitmore Mountains: A Displaced Fragment of the Gondwanian Fold Belt

The Ellsworth Mountains form a NNE–SSW trending mountain range 415 km long that contains the highest mountain in Antarctica. The mountains are situated along the northern periphery of the Ellsworth Whitmore Mountain crustal block which represents part of a displaced terrane once situated along the palaeo-Pacific margin of Gondwana prior to supercontinent break-up adjacent to South Africa and the Weddell Sea coast of East Antarctica. It was assembled in its present position by Late Cretaceous times, following the Middle to Late Jurassic break-up of Gondwana. Some 13 km of sedimentary succession is exposed within the Ellsworth Mountains, representing a continuous Middle Cambrian to Permian succession that was deformed during the Late Permian to Early Triassic Gondwanian folding. Such a complete succession is unusual in Antarctica and is part of the Gondwana cover sequence that has similarities to the Trans-Antarctic Mountains including the Pensacola Mountains. The Early Palaeozoic succession of the Ellsworth Mountains comprises the Heritage Group (Early to Late Cambrian) and the Crashsite Group (Late Cambrian to Devonian). The Heritage Group is composed of clastic sedimentary and volcanic rocks half the entire stratigraphic thickness within the Ellsworth Mountains. The volcanic rocks formed in a mid-Cambrian continental rift environment with mid-ocean ridge-type basalts erupted near the rift axis. The Heritage Group is overlain by 3,000 m of quartzites of the Crashsite Group, Permo-Carboniferous glacial diamictites of the Whiteout conglomerate and the Permian Polar Star Formation. Middle Jurassic granites related to Gondwana break-up intrude the Ellsworth Mountain succession in scattered nunataks throughout the remainder of the Ellsworth Whitmore Mountain crustal block.

17.4.3 Thurston Island: Pacific Margin Magmatic Arc

The Thurston Island block, which includes Thurston Island on the adjacent Eights Coast and Jones Mountains, records Pacific margin magmatism from Carboniferous to Late Cretaceous times. The igneous rocks form a uniform calc-alkaline suite typical of subduction settings. On Thurston Island, the observable history began with Late Carboniferous (390 Ma) emplacement of granitic protoliths of orthogneiss. Cumulate gabbros were emplaced soon after gneiss formation, followed by diorites that have Triassic ages. In the nearby Jones Mountains, the oldest exposed rock is muscovite-bearing granite with an Early Jurassic age of 198 Ma. The subsequent evolution of the Thurston Island area was dominated by Late Jurassic and Early Cretaceous bimodal suites. Between 100 and 90 Ma, volcanism in the Jones Mountains became predominantly silicic prior to cessation of subduction along this part of the margin by collision or interaction of a spreading ridge with the trench. In the Jones Mountains, the basement rocks are unconformably overlain by post-subduction Miocene alkalic basalts.

17.4.4 Marie Byrd Land: Pacific Margin Magmatic Arc

Small scattered exposures throughout the coastal parts of Marie Byrd Land suggest that the block may contain two geological provinces or superterranes. In the western part, the oldest Palaeozoic rocks are a thick uniform sequence of folded sandstone-dominated quartzose turbidites of the Swanson Formation. In the eastern part, the older basement rocks include biotite paragneiss, calc-silicate gneiss, marble, amphibolite and granitic orthogneiss with protolith ages of 504 Ma. In western Marie Byrd Land, the Swanson Formation was intruded by the Devonian–Carboniferous Ford Granodiorite and Cretaceous granitoids, whereas in eastern Marie Byrd Land, magmatic rocks are predominantly Permian and Cretaceous in age indicating a long-lived magmatic history for Marie Byrd Land. The Cretaceous magmatic rocks include mafic dyke suites and anorogenic silicic rocks, including syenites and peralkaline granites that record an important change in the tectonic regime from a subducting to an extensional margin, prior to separation of New Zealand from Marie Byrd Land and sea floor spreading from 84 Ma.

17.4.5 The Antarctic Peninsula: Long-Lived Andean-Type Margin

The Antarctic Peninsula is a long-lived magmatic arc built at least in part on continental crust with a record of magmatism and metamorphism that stretches back at least to Cambrian times (Leat et al. 1995; Miller et al. 2001). Pre-Mesozoic rocks are only sparsely exposed and include orthogneisses with protolith ages of c. 450–550 Ma, paragneisses that form the basement to Triassic granitoids no older than Late Cambrian and a few small granitic bodies c. 400 Ma. Locally, the basement underwent metamorphism, migmatization and granite emplacement during Carboniferous (c. 325 Ma) and Permian (c. 260 Ma) times.

The Mesozoic geology of the Antarctic Peninsula has traditionally been interpreted in terms of a near-complete arc trench system with Mesozoic accretion subduction complexes on the western Pacific margin of the Peninsula, a central magmatic arc active from 240 to 10 Ma, represented by the Antarctic Peninsula Batholith (Leat et al. 1995), and thick back-arc and retro-arc basin sequences on the eastern Weddell Sea side (Macdonald and Butterworth 1990). The polarity of the system is consistent with east-directed subduction of proto-Pacific Ocean floor. However, the discovery of major ductile shear zones along the spine of the peninsula has led to the identification of separate domains and the possibility of the collision and accretion of separate terranes along the margin (Vaughan and Storey 2000). Triassic and Early Jurassic plutons were emplaced along the palaeo-Pacific margin of Gondwana prior to the break-up of the supercontinent. The earliest plutons were peraluminous granites with S-type characteristics. By 205 Ma metaluminous, I type granitoids were emplaced. Magmatism associated with the

Jurassic break-up of Gondwana is represented by extensive silicic volcanism and associated subvolcanic plutonism that is part of the large Gondwana-wide volcanic igneous province. Cretaceous and younger plutons were emplaced as a result of east-directed subduction of proto-Pacific ocean crust, ranging in composition from gabbro to granodiorite with a peak of activity between 125 and 100 Ma. The tertiary part of the batholith is restricted to the west coast of the northern Antarctic Peninsula, signifying a major westwards jump in the locus of the arc. With the exception of one small segment, subduction and its associated magmatism ceased in the Antarctic Peninsula between c. 50 Ma and the present day, following a series of northward-younging ridge trench collisions.

17.5 Gondwana Break-up: The Isolation of Antarctica

There were four main episodes in the disintegration of the Gondwana continent, leading eventually to the isolation of Antarctica, the development of the circum-polar current (Lawver 1992) and an Antarctic continent covered in ice. The initial rifting stage started in Early Jurassic times (180 Ma) and led to a seaway forming between West (South America and Africa) and East Gondwana (Antarctica, Australia, India and New Zealand) and to sea floor spreading in the Somali, Mozambique and possibly the Weddell Sea basins. The second stage occurred in Early Cretaceous times (circa 130 Ma) when this two-plate system was replaced by three with South America separating from an African-Indian plate and the African-Indian plate from Antarctica. In Late Cretaceous times (90–100 Ma), New Zealand and South America started to separate from Antarctica until finally approximately 32 Ma, the break-up of that once large continent was complete when the tip of South America separated from the Antarctic Peninsula by opening of the Drake Passage allowing the formation of the circum-polar current and thermal isolation of Antarctica.

17.5.1 The West Antarctic Rift System

Although the final isolation of Antarctica did not occur until opening of the Drake Passage c. 32 Ma, a rift system formed within West Antarctica during Tertiary times (Behrendt et al. 1991). The rift system extends over a 3,000 × 750 km largely ice covered area from the Ross Sea to the Bellinghausen Sea, comparable in area to the basin and range and the East African rift systems. A spectacular rift shoulder scarp along which peaks reach 4–5 km maximum elevation extends from northern Victoria Land to the Ellsworth Mountains. The rift shoulder has a maximum present-day physiographic relief of 7 km in the Ellsworth Mountains–Byrd Subglacial Basin area. The Trans-Antarctic Mountain part of the rift shoulder has been rising episodically since Late Cretaceous times. The rift system is characterized by bimodal, mainly basaltic alkali volcanic rocks ranging in age from Oligocene or earlier to the present day. The large Cenozoic volcanic centres in Marie Byrd Land have been related to a mantle plume. Sedimentary basins within the rift system in the Ross Sea embayment contain up to 15 km of Tertiary sediments that preserve a record of climate change from a greenhouse to an ice house world. There are 18 large central vent volcanoes in Marie Byrd Land that rise to elevations between 2,000 and 4,200 m above sea level.

17.6 Antarctic Climate History: The Past 100 Million Years

The large-scale palaeogeography of the Antarctic region varied little from Late Cretaceous to Eocene times, with the Antarctic continent still connected to South America and Australia and in a polar position (Barrett 1999). The West Antarctic rift system had begun to develop in the Late Mesozoic with uplift in the Palaeocene as the Trans-Antarctic Mountains began to rise and steadily erode. The earliest evidence of glaciers forming on the Antarctic continent comes as sand grains in fine-grained uppermost Lower Eocene and younger deep sea sediments from the South Pacific with isolated sand grains interpreted to record ice-rafting events centred on 51, 48 and 41 Ma. In the Ross Sea area close to the Trans-Antarctic Mountains, glaciers were calving at sea level in Eocene time becoming more extensive and spreading in Early to Late Oligocene characterized by a number of thin till sheets separated by thin mudstone intervals. One of the mudstones contains a Nothofagus leaf which along with contemporaneous beech palynomorphs indicates a cool temperate climate on land during interglacial episodes with many episodes of temperate ice sheet growth and collapse. There was progressive disappearance of the Nothofagus-dominated flora by Late Oligocene times.

By Early Miocene times, the Antarctic was completely isolated with the development of the vigorous circum-polar currents, and the present topography of the continent was in place. There was a large increase in ice cover beginning around 15 Ma. Since the Middle Miocene, Antarctic temperatures have remained close to their present levels and the East Antarctic ice sheet has been a semi-permanent feature during the last 15 million years (Barrett 1999). This view is supported by recent work on well-preserved ice desert landforms and deposits in mountains at the head of the Dry Valleys. These are dated from fresh volcanic ash deposits ranging between 4 and 15 Ma, indicating that mean annual temperatures have been no more than 3 °C above present at any time in the Pliocene. These and the geomorphic data suggest an enduring polar ice sheet since Middle Miocene times. However, a different post-Middle Miocene view of the behaviour of the East Antarctic ice sheet has been presented as a consequence of finding a diverse biota of diatoms, sponge spicules, radiolarian, palynomorphs and foraminifera in glacial diamictites or till deposits named the Sirius Group at a number of locations high in the Trans-Antarctic Mountains. The biota include marine diatoms of Pliocene age which may have been deposited in seas in the East Antarctic interior, subsequently

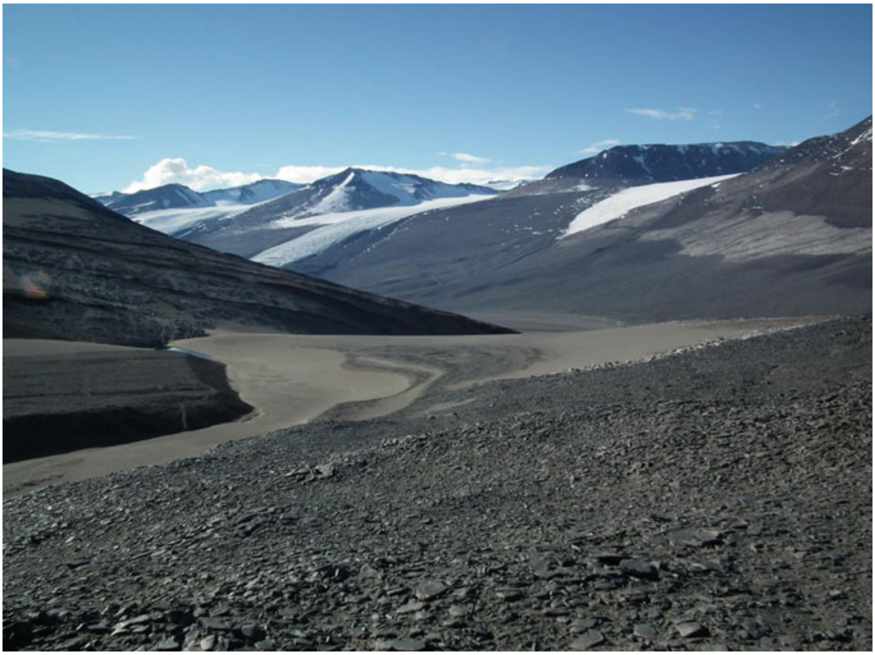

Fig. 17.3 A McMurdo Dry Valley landscape showing a range of surface features including wind-blown sand, glacially scoured rock surfaces and glacial debris

to be glacially eroded and transported to their present sites by an enlarged East Antarctic ice sheet. Although the transport processes and depositional setting for the tills are well established, the origin of the age-diagnostic microfossils found in them has been in dispute. It is likely that some of the Pliocene-age-diagnostic diatoms were deposited from the atmosphere and may not be used to date the associated deposit. The Sirius Group also includes terrestrial sequences recording many advances and retreats of inland ice through the Trans-Antarctic Mountains. The uppermost strata include shrubby vegetation that indicates a mean annual temperature 20 degrees warmer than present day. As the flora is long-ranging, the precise age of these deposits is not known.

The cyclical pattern of ice volume change through the Quaternary is well established from the deep sea isotopic records and inferred from ice core studies for the past 400,000 years from ice cores taken from near the middle of the East Antarctic ice sheet at Vostok Station. It shows a cyclical advance and retreat at 100,000-year intervals and that temperatures in the Antarctic interior were the same as today's during the last interglacial and then fell episodically to allow about 10 degrees cooler during the Last Glacial Maximum followed by a rapid rise to Holocene temperatures around 10,000 years ago.

Over many millions of years, ice has had a dramatic effect on the underlying geology and landscape (Fig. 17.3), on the one hand eroding and polishing the rock surfaces, and on the other hand depositing rock debris and blankets of glacial drift or distinctive moraine features on the landscape (Fig. 17.3). These features help to demarcate previous high stands or periods of stable ice, enabling us to define the extent of previous glaciations. Some Antarctic landscapes have been exposed for many millions of years, for example, the Dry Valleys, whereas other parts of the Antarctic landscape have only been exposed since the Last Glacial Maximum approximately 15,000 years ago. Moreover, Antarctic ice has served to change the chemistry of the substrate as it mixes, transports and deposits material away from its source and over older landscapes enabling the development of Antarctic soils and substrates suitable for colonization. The development of soils in Antarctica is dependent on many physiochemical factors including the age of the landscape, local climate conditions and the local physical and chemical environment.

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