

3 Alpine and Arctic Soil Microbial Communities

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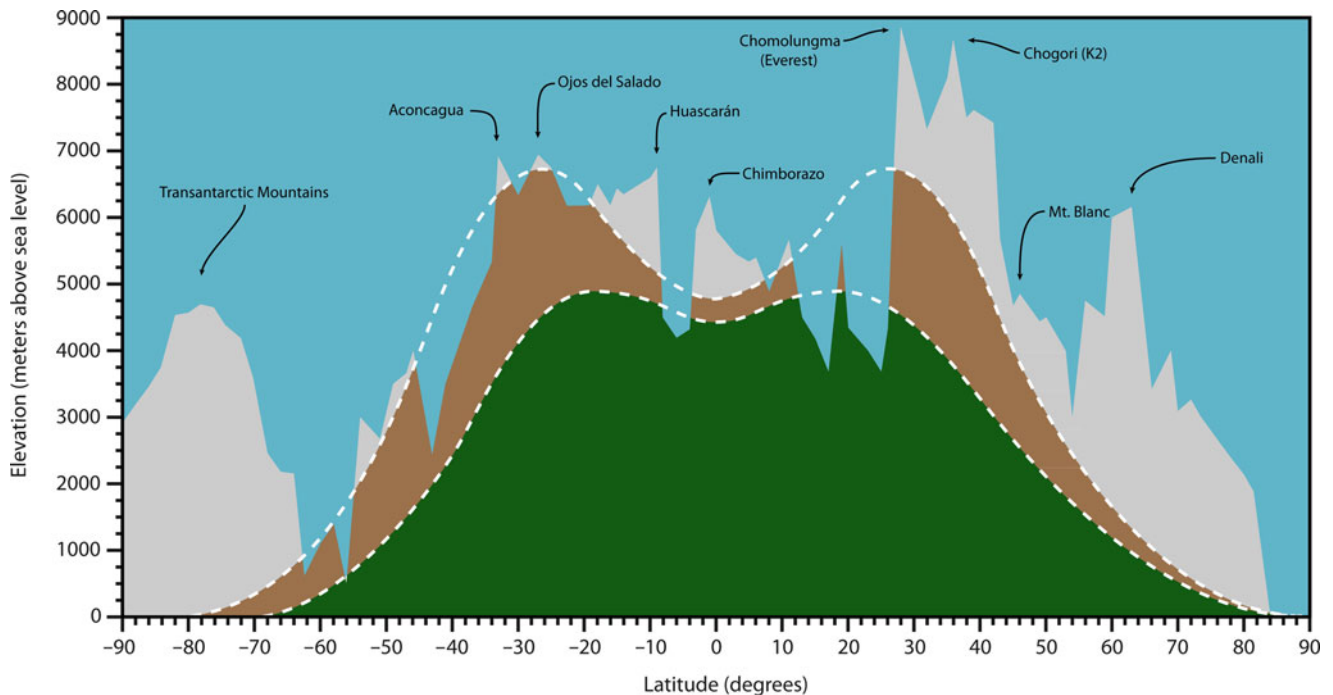
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Introduction

Cold environments, where average daily air temperatures are below 5 °C throughout the year, are widespread in the terrestrial biosphere (Zakhia et al. 2008). These ecosystems are common in high mountain ranges, the high Arctic and Antarctica. In these areas, cold temperatures are often accompanied by freeze-thaw cycles, seasonally high solar radiation exposure, low nutrient supply, limited water availability, and high salinity. As a result of these conditions, such environments are mostly devoid of higher plants and are instead dominated by microbial communities. These areas have been referred to as the subnival zone, cold deserts, the allobiosphere, or the aeolian zone among other names (Bahl et al. 2011; Edwards 1988; King et al. 2008; Mayilraj et al. 2005; Swan 1992). Due to the absence of plants and large animals, comprehensive studies of the diversity of these ecosystems have been limited. However, recent advances in molecular

techniques have allowed for more extensive study of the microorganisms that are abundant in these seemingly barren areas. High mountain cold desert areas are also receiving recent attention because they are in watersheds that are the source of water (from snow and ice melt) for a large proportion of the world's population, especially in areas downstream from the Andes, Rockies, and Himalayan Ranges. For example, the Himalayan-Karakorum-Hindu Kush Mountain complex provides water for approximately 1.3 billion people (Hua 2009). In addition, the global extent of cold, plant-free ecosystems is presently expanding rapidly as a result of glacier and ice cap melting due to global warming (Bradley et al. 2006; Byers 2007; Racoviteanu et al. 2008).

In this chapter, we review and synthesize information about bacterial and archaeal communities from high-latitude and high-elevation ecosystems across the globe. The relationship between latitude and elevation in demarcating the plant-free zone is illustrated in Fig. 3.1, which shows the approximate relationship of the upper and lower boundaries of the cold deserts with regard to latitude. The highest elevation plant-free ecosystems occur in the horse latitudes (approximately 30° north or south latitude), which are high-pressure zones that also contain the highest mountains on Earth, e.g., parts of the Andes, Karakorum, and Himalayan ranges (Fig. 3.1). Despite the overall simplicity of Fig. 3.1, cold, plant-free ecosystems can have different microclimates and, therefore, the ecological barriers to plant establishment can vary depending on wind speeds, slope and aspect among other environmental variables (Ley et al. 2004). There are three main ecosystem types at extreme latitudes and elevations (Schmidt et al. 2012): (1) Exposed soils (usually windblown) that are devoid of snow cover for most of the year and are too cold or dry for plant growth. (2) Long duration snow packs ("snow-bank soils") that are covered with snow for more than 10 months each year making it impossible for plants to complete their life cycles. (3) Recently deglaciated (early successional), undeveloped soils that may eventually be colonized by plants, at least in regions with milder climates. It is useful to distinguish between these ecosystem types because the microbial communities that are adapted to cold, dry soils are very different from those found in snow bank soils or early successional soils (Schmidt et al. 2012). Despite the inability of plant life to colonize these areas, evidence suggests that all three ecosystem types described above have intermittently active microbial communities.



■ Fig. 3.1

The figure shows the relationship between latitude and elevation in determining the elevation limits for the mostly plant-free “cold deserts” (brown) discussed in this chapter. Vegetated regions are shown in green and permanently ice-covered regions in light gray. Negative latitudes represent the Southern Hemisphere. Boundaries between zones are approximate because they can vary dramatically even in one mountain range due to slope and aspect and distance from large bodies of water. The highest mountains in each region are marked for reference. The elevation estimates were obtained by searching latitudinal transects for mountain ranges and identifying the highest peaks in those ranges using the Google Maps Elevation API, and estimates for the latitudinal limits of plant distribution were obtained from Smith and Poncet (1985)

Although alpine and polar habitats share many common attributes (see above) there are also important differences. For example, the angle of solar insolation, partial pressure of gases, the extent of permafrost, and the duration of the growing season all vary markedly between alpine and polar environments (Nemergut et al. 2005; Richardson et al. 2003). Photoperiods are also very different in polar and alpine environments, as very high-latitude polar regions can receive up to 24 h of daylight in the summer, while mid-latitude alpine areas receive less than 15 h (Richardson et al. 2003). These differences result in greater fluctuations in temperature in alpine regions, especially in the summer when soils can freeze at night and warm up to above 55 °C during the day (King et al. 2010a; Lynch et al. 2012; Schmidt et al. 2009). In addition, alpine regions are often characterized by low relative humidity and steep slopes that enhance runoff, both of which increase moisture stress (Richardson et al. 2003). Other similarities and differences between polar and alpine regions are reviewed in Nemergut et al. (2005).

We focus here on describing the prokaryotic diversity of cold desert systems with emphasis on areas that are mostly devoid of plants due to extreme dryness (category 1, described above). A review of fungi in extreme cold environments has been

recently published (Schmidt et al. 2012). Interest in these environments has exploded in recent years because they represent some of the most extreme terrestrial environments on Earth and are seen by some as the best analogs for Martian soils (Lee et al. 2011; Lynch et al. 2012; Schmidt et al. 2011b).

Site Descriptions

High Alpine

High-elevation cold deserts can be found in all of the major mountain ranges on Earth (Fig. 3.1), but are especially prevalent in the vast ranges of the Andes and Himalayan-Karakorum-Hindu Kush complex. Due to topographic heterogeneity and climatic variability the reasons for the lack of plants in high-elevation environments can vary dramatically as described above. In wetter regions such as the Alps and parts of the Rocky Mountains, the long duration of snow cover can limit plant establishment (“snow bed” communities) even when there is enough moisture to support plant growth. However, true high-elevation cold deserts mostly exist in drier regions

where the duration of snow cover is reduced and soils are exposed to drying winds, temperature fluctuations, and high levels of solar radiation for most of the year. The reality of climate change can further confound our understanding of high-elevation ecosystems, in that recent rapid retreat of glaciers has exposed large areas of new soils that may or may not eventually be colonized by plants, depending on long-term patterns of moisture availability (Nemergut et al. 2007).

Much of our current understanding of high-elevation cold soils comes from studies done at the Niwot Ridge Long-Term Ecological Research (LTER) site in the Colorado Rocky Mountains. The range of microenvironments at this site is wide and encompasses a continuum of snow bed to wind scoured, low snow habitats (King et al. 2010b; Ley et al. 2004). Most work at this site has been focused on the wetter end of this spectrum where soils are covered with snow for up to 10 months of the year and are only snow-free during the driest parts of the year (late summer and early fall). These sites contain complex microbial communities including multiple trophic levels of eukaryotes as described elsewhere (Freeman et al. 2009a, b). Early successional, high-elevation systems have been mostly studied in the European Alps, where plant colonization can be fairly rapid (Edwards et al. 2006; Miniaci et al. 2007). However, recent work on early successional soils in dry regions of the Andes is providing new insights into the earliest microbial stages of succession in the absence of plant invasion (Nemergut et al. 2007; Schmidt et al. 2008). Finally, the most extreme high-altitude environments studied to date are soils on the flanks of the largest volcanoes on Earth, in the Atacama region on the border between Chile and Argentina (Costello et al. 2009). The combination of the elevation (>6,000 m.a.s.l.) and the aridity of the region make these some of the most oligotrophic and lowest diversity unglaciated, surface environments on Earth (Lynch et al. 2012). The present chapter focuses mostly on cold deserts of high alpine ecosystems with comparisons to polar deserts whenever possible.

Antarctica

Only about 0.4% or roughly 56,000 km² of the Antarctic continent is ice free. Of the 56,000 km², the McMurdo Dry Valleys account for more than 15% of the ice-free ground representing both the largest contiguous expanse of ice-free landscape and the best studied in terms of microbiology (Bockheim and McLeod 2008; Cary et al. 2010). The Dry Valleys are located in Southern Victoria Land along the western coast of McMurdo Sound and they remain ice free largely due to the presence of the Trans-Antarctic mountain range that blocks the flow of the East Antarctic Ice Sheet (Bockheim and McLeod 2008). Much of the remaining ice-free portions of Antarctica occur either along or near the coast or at high elevations in the Ellsworth, Transatlantic, and North Victoria Land mountains.

As with the other cold deserts reviewed in this chapter, inhabitants of the Dry Valleys are challenged with frigid temperatures (mean annual temperatures range from -15°C to -30°C), fluctuating temperatures (temperature fluctuations exceeding 20°C are common), high UV radiation, low precipitation (less than 10 cm a year) and limited water availability (<2% soil water content) (Marchant and Head 2007; Smith et al. 1992; Vincent 1988). In addition these challenges are compounded by the often gale force katabatic winds that further desiccate the landscape and the high salt content of the soils (Claridge and Campbell 1976). It is for these reasons that the Dry Valleys represent one of the least hospitable environments on Earth and are often considered to be one of the coldest and driest deserts on the planet (Hopkins et al. 2006; Onofri 2004). Nevertheless, the Dry Valleys are home to a diverse assemblage of bacterial taxa and a limited number of Eukaryotes (see below and Cary et al. 2010).

The Arctic

Although tundra has received the most attention in past research, polar deserts constitute a major component of the Arctic comprising 44% of the Canadian high Arctic (Bliss and Gold 1999). Compared to other Arctic habitats, floral and faunal diversity and abundance are markedly lower in the Arctic deserts where growing seasons are about 2 months long (Bliss 1981). Like other cold deserts, Arctic deserts are characterized by limited moisture, extremes of temperature, UV radiation, nutrient limitations, and cryogenic disturbance (Cockell and Stokes 2006; Dickson 2000). Sorted and non-sorted polygons and soil stripes are common formations of patterned ground in these systems (Bliss 1981). While mosses predominate over lichens and vascular plants in total cover, both vascular plant and cryptogamic cover typically remain at <5% (Bliss 1981; Bliss et al. 1984; Bliss and Gold 1999). As a result, Arctic deserts display levels of soil organic matter, vegetation biomass, and net primary production one to three orders of magnitude lower than other already highly constrained Arctic ecosystem types (Callaghan et al. 2004). Nonetheless, the presence of sparse vascular plant cover in addition to lichens and moss stands in contrast to the Dry Valleys of Antarctica and the extreme high-elevation sites reviewed in this chapter. However, there are completely plant-free areas in the high Arctic, but it is not clear if these areas are just early successional stages that will eventually be colonized by plants.

Microbial Biomass and Activity

The first published description of the Dry Valleys of Antarctica by Captain Robert Falcon Scott in 1903 captured the seemingly lifeless nature of this and other cold desert landscapes where he noted the virtual absence of vascular plants, mosses, and even lichens (Scott 1905). The earliest studies of cold deserts in alpine

and polar systems focused primarily on the visible accumulations of organic matter including seasonal streams, endoliths, and ice-covered lakes (Friedmann 1982; Friedmann et al. 1993; Green et al. 1989; McKnight 1989; Swan 1963). When focus shifted to the barren soils, the largely culture-based surveys revealed an exceptionally low abundance and diversity of bacteria (e.g., 10^2 – 10^4 g⁻¹, reviewed in Cowan and Tow 2004). Conversely, more sensitive ATP-based assays suggest cellular densities several orders of magnitude higher at 10^6 – 10^8 prokaryotic cells g⁻¹ (Cowan et al. 2002). Other recent efforts to quantify microbial biomass using the chloroform fumigation method have shown that dry sites in Antarctica and the high Himalayas (>5,500 m.a.s.l.) have biomass levels averaging about 20 µg microbial carbon per gram of soil (Ball et al. 2009; Schmidt et al. 2011b). At extreme high-elevation sites (>6,000 m.a.s.l.) in the Atacama region, Lynch et al. (2012) found microbial biomass levels of zero to 60 µg C g⁻¹ using the same technique. For comparison, the biomass levels measured at these three extreme sites are two to three orders of magnitude lower than levels found in forest or tundra soils, and an order of magnitude lower than biomass levels in wetter (but plant-free) high-altitude soils of Colorado and Perú (King et al. 2008).

Despite the recent studies reporting measurable levels of microbial biomass in the most extreme cold desert soils on the planet (Ball et al. 2009; Lynch et al. 2012; Schmidt et al. 2011), it is still not clear how active these microbes are. In addition, the origin of the soil organic matter in these soils is unclear. Initial speculation centered on the Aeolian deposition of material from the more organic rich areas in the vicinity (Horowitz et al. 1972; Swan 1992). However, more recent isotopic analysis of the Antarctic Dry Valley organic matter suggests a limited role for present day aeolian redistribution of lacustrine carbon. Instead the data suggest that legacy carbon from late Wisconsin paleoenvironments and accumulation of autotrophic carbon fixation though the subsequent millennia account for the majority of current soil carbon stocks (Burkins et al. 2000; Moorhead et al. 1999). Furthermore, many cold desert soils harbor cyanobacteria, which can ostensibly power in situ photoautotrophic primary productivity (Freeman et al. 2009b; Novis et al. 2007; Starkenburg et al. 2011). Finally, the possibility of chemolithotrophic carbon fixation has not been adequately addressed in these systems, it is hinted at by the presence of putatively chemoautotrophic Thaumarchaeal and mixotrophic Actinobacterial sequences (Lynch et al. 2012; Tiao et al. 2012; Yergeau et al. 2007) and by limited studies in Arctic deserts when iron and sulfur compounds are prevalent (Borin et al. 2010).

Even in some of the most arid high alpine and Dry Valley sites, soil CO₂ flux is in fact measurable and estimates of mean residence time of C in Taylor Valley soils were on the order of 20 years indicating some in situ carbon fixation (Burkins et al. 2001; Parsons et al. 2004). Furthermore, although limited, recent culture-independent diversity assays have also shown that cold desert soils harbor previously underestimated diversity and unique prokaryotic community structures (see below and Lynch et al. 2012; Niederberger et al. 2008; Smith et al. 2006; Schmidt et al. 2011; Yergeau et al. 2007). It therefore appears

likely that cold desert microbial communities are more complex and active than previously thought. Nevertheless, it remains to be seen which components of these systems are active and to what extent the heterotrophic community is dependent on endogenous autotrophy.

Microbial Diversity of Cold Desert Soils

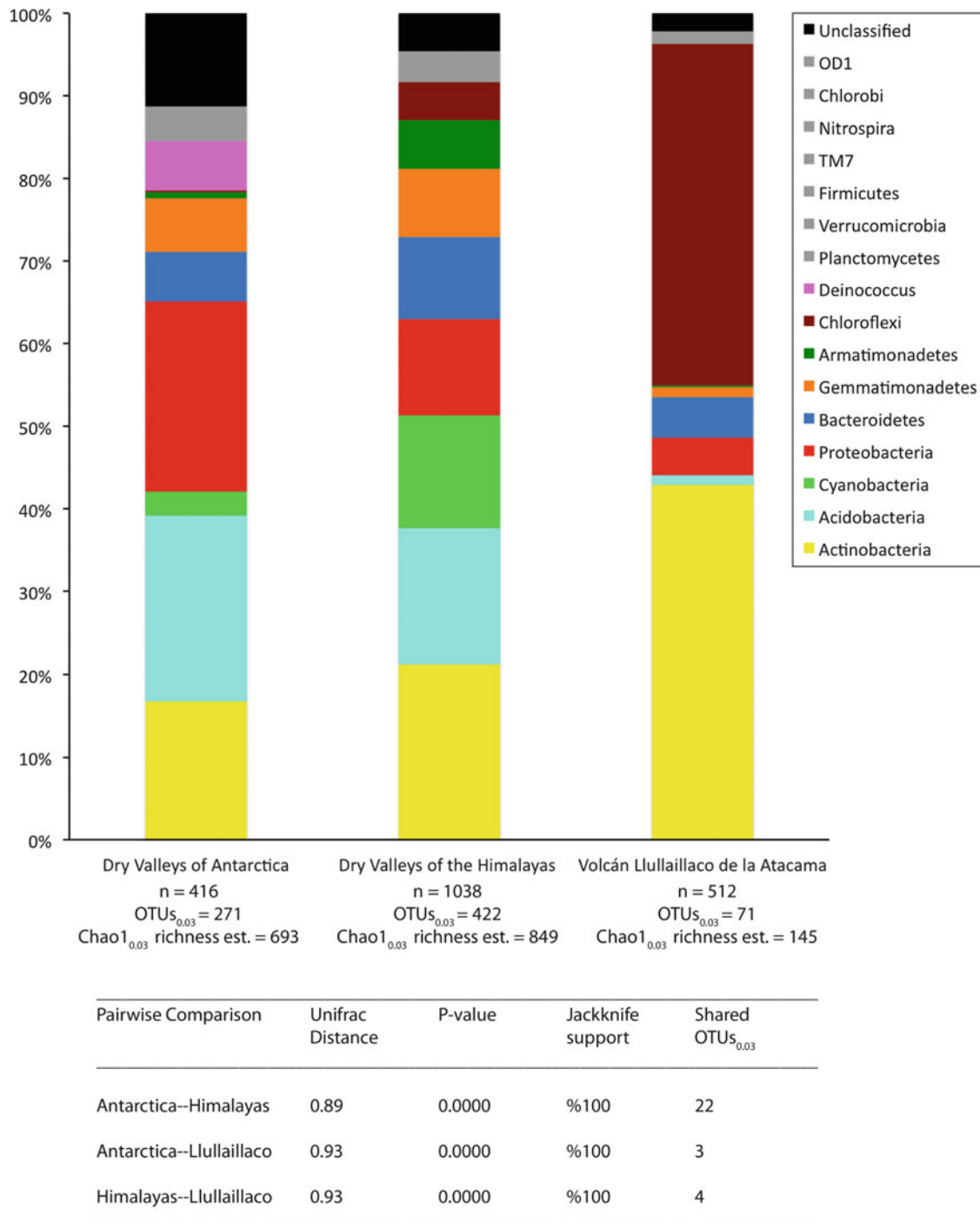
In this section, we give a brief overview of recent research on the microbial diversity of cold desert soils and then compare diversity across these environmentally similar, but geographically distant habitats.

Alpine

Culture-independent surveys of plant-free, high-elevation soils of the Rocky Mountains indicate that these heavily snowpack-impacted soils have a very high level of bacterial diversity approaching that of soils from temperate vegetated areas (Costello and Schmidt 2006; Freeman et al. 2009b; King et al. 2010b). However, drier high-elevation habitats have much lower bacterial diversity. For example, culture-independent surveys of high-elevation mineral soils from the dry valleys of the Himalayas, Vólcan Llullaillaco, and Vólcan Socompa show much lower levels of diversity (Costello et al. 2009; King et al. 2010b; Lynch et al. 2012)—very similar to the diversity of bacteria in the Dry Valleys of Antarctica (🔍 Fig. 3.2). The dominant groups of bacteria in cold deserts of the high Himalayas are Actinobacteria, Acidobacteria, and Cyanobacteria; whereas the dominant bacteria in the high Andes (Vólcan Llullaillaco) are Actinobacteria and Chloroflexi (▶ Fig. 3.2). The apparent absence of Cyanobacteria on Vólcan Llullaillaco (Lynch et al. 2012) and the driest sites on Vólcan Socompa (Costello et al. 2009) is unique for a plant-free soil and Lynch et al. (2012) speculate that the dryness, high elevation, and extreme UV flux on Llullaillaco make it unsuitable for photosynthetic life. Another intriguing finding from the high Andes is the unusually high percentage of Chloroflexi in 16S libraries (Costello et al. 2009; Lynch et al. 2012). Most of the phylotypes in this group have no close relatives in low-elevation habitats but some are related to undescribed phylotypes that inhabit cold, plant-dominated high-elevation ecosystems (Costello and Schmidt 2006; Freeman et al. 2009b).

Antarctica

Like the alpine, the community structures of the Antarctic Dry Valleys are fairly unique compared to more temperate soils in that representative sequences of only 14 bacterial phyla have been recovered, with the Actinobacteria, Acidobacteria, and Gammaproteobacteria dominating (🔍 Fig. 3.2), and significantly fewer Alphaproteobacteria than most temperate soils (Cary et al. 2010; Niederberger et al. 2008;



■ Fig. 3.2

Proportional phylum-level representation of select bacterial 16S rDNA libraries from Antarctica and alpine barren mineral soils classified using the approach of Wang et al. (2007). Clustering analysis and Chao1 richness estimates (Schloss et al. 2009) highlight the low overall alpha diversity, particularly from the high-elevation sites (>6,000 m.a.s.l.) on Vólcan Llullaillaco. Despite the broad level similarities between these communities, Unifrac analysis (Lozupone and Knight 2005) shows how little total branch length is actually shared between communities, which is much less than would be expected by chance. Data are from (Aislabie et al. 2006; King et al. 2010a, b; Lynch et al. 2012; Niederberger et al. 2008; Schmidt et al. 2011a; Smith et al. 2006)


Smith et al. 2006). Culturing efforts also confirm the importance of the Actinobacteria with *Corynebacterium*, *Achromobacter*, and *Arthrobacter* spp. making up the majority of isolates, and

Micrococcus, *Planococcus*, *Streptomyces*, and *Nocardia* also present (Cameron et al. 1972). Interestingly, most bacterial mineral soil isolates are psychrotrophic, although psychrophiles and

mesophiles are also readily isolated (Cowan and Tow 2004). This makes sense since psychrotrophs are more likely able to cope with the temperature cycles experienced in the mineral soils, while true psychrophiles are better suited to the more stable permafrost.

The prokaryotic communities seemingly have only one or two trophic levels, depending on the degree of water stress (Smith et al. 2006; Niederberger et al. 2008). In the more productive soils, the prokaryotes also support a third level of bacterivorous protists and nematodes. The milder and wetter Dry Valley soils clearly harbor cyanobacteria, which can ostensibly power in situ photoautotrophic primary productivity (Novis et al. 2007; Vincent 2000). In the driest of Antarctic soils where cyanobacteria are less abundant, local carbon fixation may seem less likely; however, the possibility of chemolithotrophic carbon fixation has never been addressed. The presence of putatively mixotrophic Thaumarchaeal and Actinobacterial sequences certainly hints at this possibility (Bates et al. 2011; Tiao et al. 2012; Yergeau et al. 2007).

Arctic

Unexpectedly, recent culture-independent 16S rRNA studies have demonstrated that the degree of diversity displayed by high-Arctic tundra microbial communities is similar to that of soils from temperate latitudes (Chu et al. 2010; Neufeld and Mohn 2005). Evidence from some of the drier areas of the Arctic confirm this trend by revealing high diversity and species turnover (Schütte et al. 2010); by rough estimates Arctic desert microbial diversity in some cases appears to be as high as that of other Arctic ecosystems (Torsvik et al. 2002). It is presently unclear why Arctic polar deserts seem to have higher levels of microbial biodiversity than the driest areas of Alpine and Antarctic deserts, but overall the more maritime-influenced climate of most of the high Arctic may be partially responsible (Omelon et al. 2006). However, some inland sites of the high Arctic show somewhat decreased levels of diversity and a predominance of Actinobacteria and Acidobacteria (Cockell et al. 2001; Schütte et al. 2010) as has been observed in some of the driest cold deserts of Antarctica and the Andes (compare to  Fig. 3.2).

Microscopy-based studies of Arctic desert soils have revealed an abundance of cyanobacteria, including members of the Nostocales, Chroococcales (*Gloeocapsa*), and Oscillatoriales (*Lyngbya*, *Phormidium*) (Cockell and Stokes 2006; Dickson 2000). Therefore, cyanobacteria are likely responsible for a dominant portion of primary production in Arctic deserts (Cockell and Stokes 2006). In addition, cyanobacteria, in particular *Nostoc commune*, predominate in Arctic desert soil crusts where N fixation rates can be as high as those of vegetated systems (Dickson 2000). Thus, N-fixing cyanobacteria are likely the primary source of biological N-inputs in Arctic deserts (Dickson 2000; Zielke et al. 2005). Overall, while molecular techniques in evaluating bacterial community diversity are being applied to Arctic ecosystems, little molecular research has specifically focused on cyanobacteria in Arctic deserts. The

biogeography of cyanobacteria in Arctic cold deserts is discussed below in comparison to alpine and Antarctic sites.

Biogeography and Limiting Factors for Cold Desert Prokaryotes

The continued accumulation of culture-independent sequences from cold desert soils across the globe is providing some preliminary glimpses into the biogeography and factors that limit microbial life in these systems. In this section, we will briefly review some of this accumulating data and give specific examples of new insights being gained from these studies. Specifically, we will focus on two of the dominant groups found in cold desert soils, the Actinobacteria and Cyanobacteria; and a group that is extremely understudied in these systems, the Archaea.

Biogeography and Limiting Factors for Cyanobacteria

In recent studies of high alpine ecosystems throughout the world, cyanobacteria were found to dominate many less xeric and later successional seres of cold desert soils (Freeman et al. 2009b; Nemergut et al. 2007; Schmidt et al. 2009, 2011b). In addition, comparative studies have illustrated genetic similarities among Arctic and Antarctic aquatic cyanobacteria (Jungblut et al. 2010) as well as habitat distributions of cyanobacteria specific to cold desert soils compared to warm deserts (Bahl et al. 2011). Furthermore, detailed phylogeographic studies are revealing that Arctic, Alpine, and Antarctic cold deserts soils share many of the same cyanobacterial and algal phylotypes (Schmidt et al. 2011b). For example, the cyanobacterial species *Microcoleus vaginatus* is common to most cold desert sites in Antarctica, the Andes, the Himalayas, and the high Arctic, yet this species complex shows significant genetic divergence patterns in analyses of all pair-wise comparisons of sites at the intercontinental scale (Schmidt et al. 2011b). In other words, this and other groups of cyanobacteria are globally distributed, yet have specific genotypes in each region. Whether these patterns are driven mostly by geographic isolation or environmental selection remains to be fully elucidated.

In the Dry Valleys of Antarctica, the presence of cyanobacteria does not follow any strict latitudinal gradient; cyanobacteria have been detected as far south as ice-free environments persist (87°S; Broady and Weinsteinz 1998). However, Namsarev et al. (2010) found that cyanobacterial diversity is apparently highest between latitudes 70°S and 80°S and they speculate that low cyanobacterial biodiversity above 70°S may be explained by the presence of vegetation cover, since plants and mosses can competitively exclude cyanobacteria. Below 80°S, however, cyanobacteria are thought to be excluded from many sites by harsher environmental conditions. More favorable conditions may exist on northern facing slopes due to an increase in soil temperature and the availability of melt water (Elster and Benson 2004). In a similar vein, although cyanobacteria have

been observed in some of the highest ice-free regions of the Himalayas and the Peruvian Andes (Schmidt et al. 2009, 2011b), the driest sites yet studied in the Andes are apparently devoid of cyanobacteria. In the hostile ice-free areas atop Volcán Socompa and Volcán Llullaillaco in the Atacama Desert, recent culture-independent surveys, HPLC pigment assays, fluorometry, and culturing efforts have found no evidence of cyanobacteria and little or no evidence of phototrophy except in areas receiving supplemental moisture (Costello et al. 2009; Lynch et al. 2012). The soil in these environments is exposed to especially high levels of solar radiation, extreme daily temperature fluctuations (up to 70 °C) and very limited water availability. It therefore appears that some terrestrial environments are simply too extreme for cyanobacteria. However, very little work has focused on potentially more resistant phototrophs such as some Chloroflexi and Rhodospirillales that are common in these systems (King et al. 2010b; Lynch et al. 2012).

Other environmental variables (besides water availability) may also influence the distribution of cyanobacteria in cold desert soils. While Niederberger et al. (2008) identified cyanobacteria exclusively in sites within the Dry Valleys with significant soil water availability; Smith et al. (2006) found cyanobacteria in Dry Valley soils with as little as 0.7% water causing them to hypothesize that atmospheric water content was a more important factor than soil water content. Likewise, Wood et al. (2008) did not observe increased cyanobacterial diversity in Dry Valley soils with higher percent water contents, perhaps indicating that other variables may help shape the Antarctic soil cyanobacterial communities. Wood et al. (2008) further showed that magnesium and manganese correlated with cyanobacterial diversity. They also note that their site with the lowest cyanobacterial diversity was high in copper in accordance with the results of Lee et al. (2011). However, Lee et al. (2011) also reported that the most important factors affecting bacterial communities were elevation (which is highly correlated with temperature) and soil conductivity (which is a proxy for soil salinity and highly correlated with water availability). Finally Wood et al. (2008) concluded that cyanobacterial distributions are partly affected by their proximity to lakes and seasonal streams suggesting that aeolian distribution affects at least cyanobacterial diversity if not the entire microbial community.

Recent manipulative work at high-elevation sites in Colorado and Perú is also shedding some light on the factors that limit phototrophic life in cold deserts. So far this work indicates that phosphorus (P) availability is the second most limiting factor (after water availability) based on nutrient addition experiments (Schmidt et al. 2011b).

Biogeography and Limiting Factors for Actinobacteria

Actinobacteria have long been known as one of the most important groups of soil bacteria and have been studied intensively in the past because of their ability to produce numerous antibiotics (Waksman 1950). They are well adapted to the soil environment

due to their hyphal growth (which allows them to grow through or around air gaps in soil) and their ability to form spores (which allows them to be easily dispersed and survive long periods of desiccation). Both of these traits are especially important in dry soils. Therefore, it is not too surprising that they dominate some of the driest soil environments yet studied (Fig. 3.2). However, the ecological role of Actinobacteria in these dry soils has received very little study and it is possible that they are only present in extremely dry habitats because their spores are so easily dispersed. In other words, they may just exist in these environments as spores that were produced elsewhere.

If Actinobacteria exist merely as dormant spores in cold desert soils, then one would expect random patterns of distribution and the same phylotypes in different soil types. However, this is not what has been found in several recent studies of cold deserts. Lee et al. (2011) examined bacterial diversity across multiple Antarctic Dry Valleys and showed that while on a phylum level the four sites were highly similar, with Actinobacteria dominating with 62–73% of all sequences, they differed considerably at lower taxonomic levels. Of the 81 species level (3% difference) OTUs belonging to the Actinobacteria only 9 were shared between more than two of the valleys. The heterogeneity of the microbial communities within the respective valleys is an indication that localized selection is occurring and that the communities do not represent solely aeolian distributions of dormant spores (Lee et al. 2011; Smith et al. 2010).

In addition, recent work by Lynch et al. (2012) indicates that some groups of Actinobacteria may be playing a pivotal role in cold desert soils. One line of evidence is the high level of diversity of the large subunit (*coxL*) of the carbon monoxide (CO) dehydrogenase gene (CODH) found in the extremely oligotrophic soils on Volcán Llullaillaco. The nearest relatives (78–95% identity) to these sequences are uncultured sequences from globally distant (Hawaii) volcanic deposits and cultured CO-oxidizing Actinobacteria (as opposed to common CO-oxidizing Proteobacteria). The hypothesis that some Actinobacteria may be oxidizing CO in these soils needs more testing but is further reinforced by the presence of 16S genes from the genus *Pseudonocardia* in the same soils. The closest relatives (GQ495403, HM445437) to these sequences are from Icelandic and Azorean volcanic deposits (Lynch et al. 2012). In addition, the dominant 16S OTU from the highest sites on Llullaillaco (>6,300 m.a.s.l.) is most closely related to *Pseudonocardia asaccharolytica* (Y08536), which can oxidize dimethyl sulfide for energy (Reichert et al. 1998).

More evidence for the importance of *Pseudonocardia*-like organisms in cold desert soils comes from a phylogenetic analysis of the *Pseudonocardia* sequences from Volcán Llullaillaco and their closest database matches (Fig. 3.3). Among the closest relatives to the Llullaillaco sequences are *Pseudonocardia antarctica* (Prabakar et al. 2004), a CO-oxidizing species (*Pseudonocardia carboxydivorans*) (Park et al. 2008) and environmental sequences from the Dry Valleys of Antarctica and the high Himalayas. Furthermore, the environmental sequences phylogenetically cluster predominantly by geographic region indicating that genetic divergence has occurred at each site,

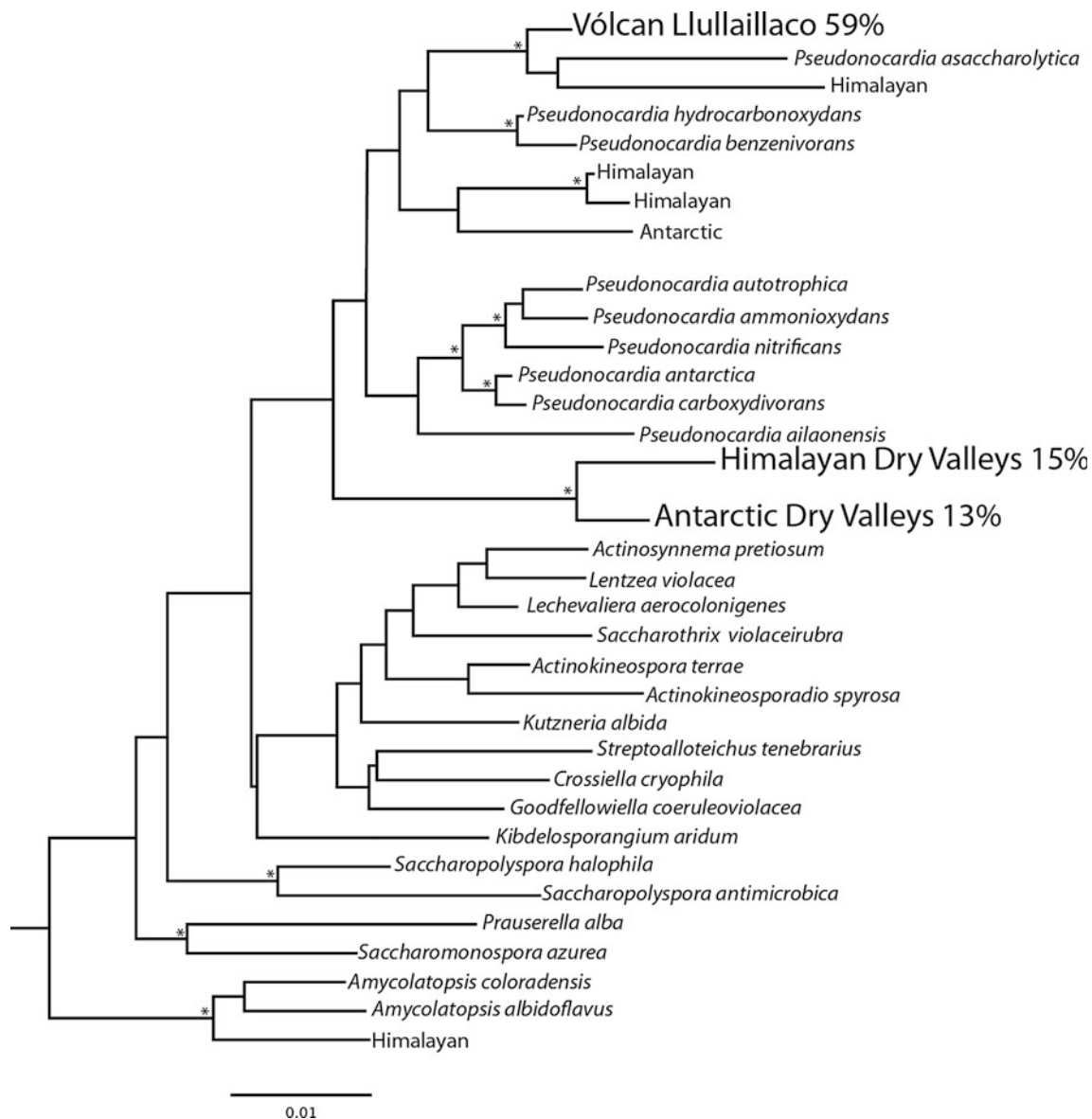


Fig. 3.3

Inferred relatedness between cultured representatives of the family Pseudonocardiaceae (Actinobacteria) and environmental Antarctic and alpine 16S rDNA sequences. Percentages indicate the proportion of Pseudonocardiaceae in the actinobacterial libraries from each region. Asterisks at nodes indicate bootstrap consistency in $\geq 75\%$ of 1,000 replicates. The tree was inferred using the SILVA database (Pruesse et al. 2007) and the neighbor-joining algorithm of MEGA5 (Tamura et al. 2011)

which implies growth and activity at each site (Fig. 3.3). Obviously, much more work is needed to establish the ecological importance of *Pseudonocardia*-like and other Actinobacteria in cold deserts, but our preliminary work indicates that they may be important players in these extreme environments.

Archaea in Cold Deserts

Compared to Bacteria, the diversity of Archaea in soils remains relatively unexplored, especially in plant-free ecosystems (Lynch et al. 2012; Zhang et al. 2009). However, Archaea may be

particularly important in cold environments. The Crenarchaeota constitute 40% of the prokaryotic biomass in cold waters of the deep oceans (DeLong et al. 1994) and may dominate large portions of the cold ocean subsurface (Biddle et al. 2006). In addition, they are consistently found in molecular surveys of soil microbial communities (Brochier-Armanet et al. 2008) including high elevation, cold soils (Oline et al. 2006; Zhang et al. 2009). Likewise, ubiquitous soil Archaea have been detected in Antarctic Dry Valley soils (Aislabie et al. 2006; Hogg et al. 2010), and a recent survey conducted by Bates et al. (2011) of Dry Valley soils consistently reported a small yet measurable presence of archaeal DNA belonging to the

Thaumarchaeota soil groups. However, the techniques employed fail to differentiate between active organisms and cryopreserved organisms and DNA. Thus it is possible that the archaeal sequences detected represent the global dispersal of soil archaea via aeolian and other processes and do not actually reflect a functioning archaeal community. Other culture-independent surveys of the Dry Valley microbial communities either opted not to target Archaea (Lee et al. 2011) or failed to detect any archaeal signal (Pointing et al. 2009). Archaeal communities have been described in Arctic permafrost environments, yet their diversity and function remain poorly studied (Steven et al. 2008; Yergeau et al. 2010) and almost no work has been done in cold Arctic deserts.

However, there have been several recent attempts to investigate the function of Archaea in high-elevation cold deserts. The presence of archaeal ammonia monooxygenase subunit A (*amoA*) genes have been studied in the high Himalayas and many plant-free areas of the Rocky Mountains (Freeman 2010; Zhang et al. 2009) and archaeal *amoA* has been found even in the highest soils examined on Mt. Everest (Zhang et al. 2009). However, the abundance of putative archaeal *amoA* decreased with altitude relative to the abundance of bacterial *amoA* perhaps indicating that bacterial ammonia oxidizers are more active at colder temperature (Zhang et al. 2009). Likewise, a majority of the archaeal *amoA* sequences found in cold desert areas of the Andes and Rocky Mountains were in the clades A4 and A6 (Freeman 2010) that are most closely related to sequences found in soils of lower elevation ecosystems (Hansel et al. 2008; Tourna et al. 2008). Obviously, much more work is needed to understand the roles of soil Archaea in cold deserts and other ecosystems.

Oases

Within all of the cold desert soil environments discussed above there exist oases that offer respite from the hostile environment. These oases include volcanic fumaroles, dead animals, seasonal streams, fractured and porous rocks, and translucent minerals. Each respective sanctuary helps mitigate specific environmental challenges and greatly alters the local microbial community. We discuss some of these briefly below because they provide unique natural experiments that may help us to understand some of the factors limiting life in cold desert soils.

Dead Animals

The remains of mummified seals have been confounding scientists and explorers since Scott's *Discovery* expedition in the early 1900s. Carcasses in varying stages of decay and preservation have been observed more than 60 km from the shoreline and 1,800 m above sea level (Banks et al. 2009; Barwick and Balham 1967; Péwè et al. 1959). The cause of these suicidal migrations remains undetermined, but their effect on the local microbial community is profound. In addition to providing a comparatively high input of organic carbon and nutrients,

the carcasses serve to retain soil humidity, stabilize soil temperature, and reduce UV radiation (Cary et al. 2010). Not surprisingly, Tiao et al. (2012) observed significant population differences (within 3 years) between a control, exposed Dry Valley site and a similar site beneath a mummified seal carcass. The seal-covered site displayed less phylogenetic diversity and maintained significant populations of only two of the seven most abundant phyla that were found at the control site. Cell densities increased at sites in direct contact with the carcass. However, the specific physiochemical changes that prompted these changes are unclear. Upon removal of the seal carcass, the previously sheltered community demonstrated a rapid decline despite the elevated levels of soil carbon and nitrogen (Tiao et al. 2012). Thus, it appears the primary benefit derived by the local microbial community from the seal carcass was the alleviation of the physical challenges and not the reservoir of nutrients.

In a similar vein, the activity of collared lemmings produces micro-oases within Arctic deserts that alter environmental conditions and microbial communities. Rotting lemming nests and scat are sources of organic matter that alter soil attributes and result in a series of feedbacks including vegetation growth (Cockell et al. 2001). Cockell et al. (2001) revealed that such micro-oases associated with lemming activity result in higher bacterial abundances, likely sustained by direct carbon inputs and resulting vegetation, as compared to the environment outside these micro-oases. The sites include cryptogamic crusts that contain N-fixing cyanobacteria, and distinct bacterial phylotypes have also been noted, such as the presence of *Enterococcus*, likely introduced from the lemming intestinal tract (Cockell et al. 2001).

Hypoliths and Cryptoendoliths

Hypoliths and cryptoendoliths are microorganisms that colonize the underside of translucent minerals and microsites within porous rocks, respectively. These rock matrices serve to shelter the community from wind and intense solar radiation (Broady 1981; Cockell et al. 2008; Cockell and Stokes 2004; Warren-Rhodes et al. 2007), increase water availability due to condensation (Warren-Rhodes et al. 2006), and buffer both temperature and humidity fluctuations (Cowan et al. 2010). The underlying geology, glacial processes, and freeze-thaw cycles have resulted in there being copious quantities of translucent rocks throughout the Dry Valleys (Broady 2005). Appropriately sized stones are, almost as a rule, colonized by hypolithic microbial communities (Cowan et al. 2010, 2011) suggesting that the generally phototrophic hypolithic communities are an important source of carbon to the region. Cowan et al. (2010) further classified the hypolithic communities into three categories, cyanobacterial dominated, fungal dominated, and moss dominated. The cyanobacterial hypolithic consortia were comprised primarily of the orders Nostocales and Oscillatoriales which accounted for approximately 45% of the cyanobacterial community. Cyanobacterial phylotypes have also been identified in the fungal-dominated hypoliths (Cowan et al. 2010).

Hypolithic communities are integral to ecosystem function in Arctic deserts where the habitat provides moisture retention, protection from UV, and temperature fluctuation. In a study of high Arctic deserts, Cockell and Stokes (2006) revealed that rocks on polygon edges were ubiquitously colonized. Dominant bacteria in these communities included microscopically identified *Gloeocapsa*, *Chroococciopsis*, *Leptolyngbya*, and *Scytonema*. Cockell and Stokes (2006) also suggest that hypolithic bacterial communities contribute heavily to Arctic desert primary productivity. Using radiolabeled carbon, they calculated productivity values of hypolithic cyanobacteria that were comparable to plant primary productivity in the high Arctic desert study site, suggesting that hypolithic bacterial communities actually double previous primary productivity estimates in Arctic deserts (Cockell and Stokes 2004).

Hypolithons have recently been identified in high altitude tundra of central Tibet underneath of quartz rocks (Wong et al. 2010). As with many of the hypolithons of the polar deserts, the communities were dominated by cyanobacteria and provide significant carbon input to the surrounding environs. Unlike other hypolithons, however, archaea in the form of unidentified crenarchaeota comprised a small yet significant (4%) fraction of the Tibetan community (Wong et al. 2010). No work has yet been done on hypolithons in the extreme deserts of plant-free areas like of high Andes or Himalayas.

The cryptoendolithic communities of the Antarctic Dry Valleys are primarily found in the Beacon sandstones which dominate the northern end of the Dry Valleys (Cary et al. 2010; Nienow and Friedmann 1993). As with the hypoliths, the cryptoendolithic environments contain a range of microbial communities (Torre et al. 2003); some are dominated by cyanobacteria and others are predominantly composed of algae and lichens. The cryptoendolithic inhabitants colonize preexisting pores in the rock at depths starting at 1 mm below the rock surface and extending up to 10 mm (Sun et al. 2010). The depth of colonization is largely determined by the degree of light penetration (Hughes and Lawley 2003; Matthes et al. 2001).

As sufficient radiation for photosynthesis and rock temperatures exceeding 0 °C are present for only a small fraction of the year, the opportunity for primary production is fleeting at best (Johnston and Vestal 1991; Sun et al. 2010). Consequently the generally warmer, north-facing exposures show increased colonization (Friedmann 1982; Kappen et al. 1981; McKay and Friedmann 1985). A further consideration is the availability of water. Unlike soil and hypolithic autotrophs, the cryptoendolithic communities do not have access to melting permafrost. The sole source of water for these communities is snow melt. Thus, the colonization sites generally occur on slopes and surfaces that lend themselves to snow catchment (Sun et al. 2010). In environments that are in immediate proximity to the cryptoendolithic communities, such as the higher elevation regions of the Taylor Valley, exfoliated cryptoendoliths can represent a significant input of organic matter and nutrients to the system (Burkins et al. 2000; Friedmann et al. 1980).

Fumaroles

From the slopes of Mt. Erebus in Antarctica, to Beerenberg in the far north, to the towering peak of Vólcan Socompa in the Andes, warm hydrothermal environments interpose themselves into some of the coldest and most arid environments on Earth. When hydrothermal systems interact with cold deserts, the effects on the surrounding environs are profound. These hydrothermal features, such as fumaroles, geysers, and hot springs, provide copious quantities of moisture, warmth, CO, CH₄, CO₂, and other potentially beneficial gases to an otherwise oligotrophic, desiccated, and frigid world. There has been some research on life inhabiting volcanically impacted soils in high alpine deserts. Costello et al. (2009) investigated the community structure of the microbial assemblages associated with high-elevation fumaroles on Vólcan Socompa. The Socompa fumaroles are relatively mild in that water vapor and gases seep through the porous soils creating patches of microbial mats and mosses in an otherwise barren landscape. Costello et al. (2009) investigated two categories of fumaroles on Socompa, warm fumaroles and cold fumaroles. The warm fumaroles raised the temperature of their surrounding environs to 25 °C and elevated the concentrations of CO₂ and CH₄ and in some areas were covered by mats of moss but were very oligotrophic where the moss had been removed by disturbance. Meanwhile, the cold fumarole soils remained at -5 °C but had increased levels of soil moisture and soil C and N and had high levels of microbial diversity with representatives from 19 phyla and subphyla dominated by the Acidobacteria, Alphaproteobacteria, Cyanobacteria, and Chloroflexi. Among these groups were microbes that could potentially participate in both nitrogen fixation and photosynthesis, suggesting that the cold fumarole environments could function as important islands of productivity within these extreme high alpine deserts. This assertion is further supported by the presence of chlorophyll *a* and an elevated soil ¹³C signature potentially indicative of the fixation of magmatic CO₂ (Costello et al. 2009).

Future Directions

While cold deserts represent uniquely extreme environments that span a geographically substantial area of the globe (► Fig. 3.1), we are only beginning to understand the dynamics of these microbial ecosystems. Recently, molecular techniques have allowed for new, higher resolution insights in microbial ecology; however, gaps in our understanding of cold desert microbiology are great compared to other biomes. Further assessing microbial community composition of these environments will provide a basis to understand patterns of community structure and function that control ecosystem process rates and ecosystem productivity in the absence of plant life. Given their relative simplicity, cold desert ecosystems have already facilitated studies of factors influencing microbial community assembly and distribution (Caruso et al. 2011; King et al. 2010b; Newsham et al. 2010; Stomeo et al. 2012), but more

comprehensive studies of these processes are needed. In addition, enhanced sequencing efforts across cold deserts may serve to help us better understand the physiology and ecology of novel taxa (especially understudied groups like the soil Chloroflexi and Archaea) and begin to sort out the biogeography of cold desert microbial distributions (Darcy et al. 2011; Schmidt et al. 2011b). Finally, cold desert environments present extreme environmental constraints that may select for microbes that best reflect life beyond our planet. Characterization of microbes, particularly those endemic to these extreme environments, will also advance perspectives in astrobiology and may uncover novel physiologies that could have application in biotechnology.

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