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# Factors promoting microbial diversity in the McMurdo Dry Valleys, Antarctica

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The McMurdo Dry Valleys (MDV) comprise a mosaic of habitats at scales ranging from micrometers to the kilometer scale. The varied landscape of the valleys, combined with strong physical and chemical gradients within and across the terrestrial and aquatic habitats, yields an ecosystem dominated by microbes that is both complex and diverse (Gordon et al., 2000; Smith et al., 2006; Mikucki and Priscu, 2007). The cold desert environment is analogous to icy conditions found on other icy worlds. For example, the low organic carbon, cold, arid soils of the MDV are similar to Mars' present-day terrestrial environment and the glaciers and ice-covered lakes of the MDV are comparable to conditions that existed on Mars in the past (Priscu et al., 1998; Wynn-Williams and Edwards, 2000; McKay et al., 2005). If there are extant or extinct life forms on Mars, they likely experience similar physical constraints and environmental challenges as do microbial communities in the MDV. Therefore, the MDV provide a unique earthly setting to gain insight into the diversity, adaptation, and function of life on other icy worlds. Here we describe the ecological processes and conditions that contribute to the microbial diversity observed in the MDV and relate these to potential life on Mars.

### **The McMurdo Dry Valley ecosystem**

The MDV include a variety of unique habitats that are connected physically, chemically, and energetically (Fig. 8.1). Solar radiation and wind are the underlying forces that determine the existence and distribution of biota throughout the valleys (Dana et al., 1998; Nkem et al., 2006). Incoming solar

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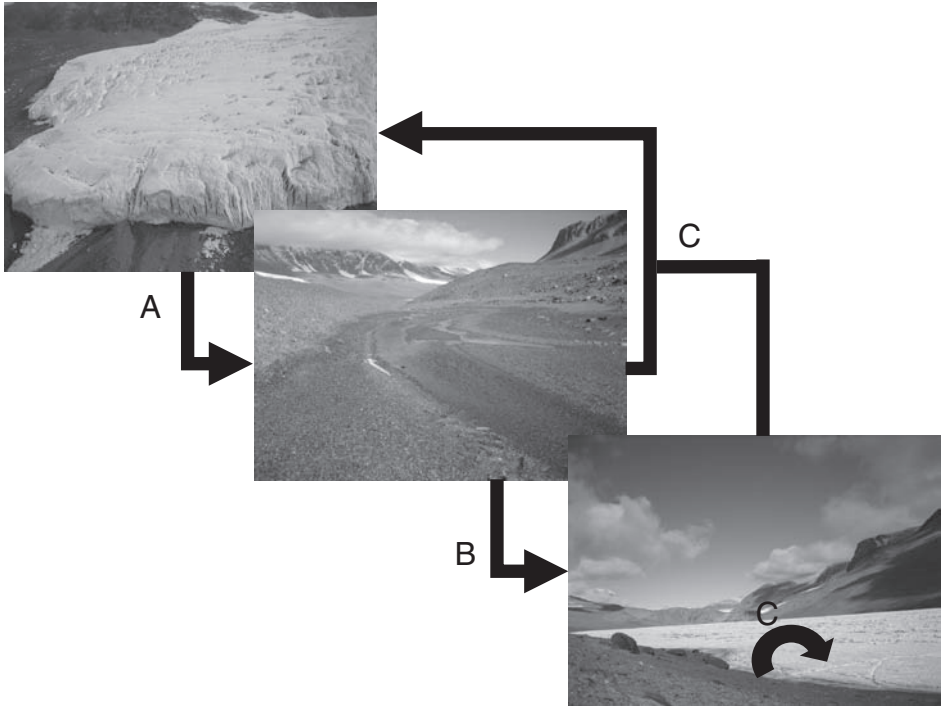


Fig. 8.1. The MDV include a variety of unique habitats that are connected physically, chemically, and energetically. Water and thermal energy are transported down the valleys from the glaciers to streams (from A) and the streams to lakes (B), whereas sediment is transferred up-valley (C, or onto lake ice), and promotes more melt and creates additional microbial habitats in the ice.

radiation is important not only for photosynthesis, but also for melting the glaciers that provide the majority of liquid water to the area (Dana et al., 1998). During 6 to 10 weeks each summer, glacial melt results in ephemeral streams, which harbor photosynthetic cyanobacterial mats and associated heterotrophic microorganisms.

Streams are significant sources of organic carbon and inorganic nutrients to the lakes they feed because of photosynthetic mat productivity and in-stream weathering of rock and sediment, and they are also a critical source of thermal input for the lakes (Vincent, 1988; Lyons et al., 1998; Spigel and Priscu, 1998; Takacs et al., 2001). Water in streams can reach temperatures of 15 °C (Conovitz et al., 1998; Cozzetto et al., 2006), making them important heat sources to the lakes (McKay et al., 2005). Liquid water columns exist within the lakes because of the annual thermal input of the ephemeral streams that essentially accumulate and transfer solar radiation from a wider surface area than the area of the lake. With the exception of Don Juan Pond in the Wright Valley, which

has salinities exceeding 600‰ due to high levels of calcium chloride (Horowitz et al., 1972), MDV lakes have permanent ice covers that serve to insulate the water column and prevent wind-driven mixing (Spigel and Priscu, 1998).

Lake ice is formed in a conveyor-belt fashion (Fritsen et al., 1998). Water freezes at the ice–water interface and is ablated at the ice–air interface (Adams et al., 1998). Less than 10% of the incident solar radiation penetrates the lake ice covers and most of this is in the blue-green part of the spectrum (Lizotte and Priscu, 1992; Howard-Williams et al., 1998). Ultraviolet radiation also penetrates the ice covers and can inhibit photosynthesis in certain lakes (Vincent et al., 1998). Wind-blown sediments deposited on the ice melts downward during summer and forms liquid water inclusions that support phototrophic and heterotrophic activity (Priscu et al., 1998). This novel microbial consortium exploits a habitat in an environment that would appear to be inhospitable for life (Paerl and Priscu, 1998).

The lakes are the sites of the highest biological activity in the MDV owing to the accumulation of nutrients, organic matter, and thermal input, and year-round constant temperatures that are above freezing (Hopkins et al., 2006). Strong physical and chemical gradients exist in the water columns, which provide a spectrum of potential habitats for the lake communities (Spigel and Priscu, 1998). In contrast are the inhospitable soils that comprise a majority of the MDV surface area (Burkins et al., 2001). Although the MDV receive up to 10 cm of moisture annually, precipitation is in the form of snow, which tends to sublimate or blow away before it melts and percolates the soils (Campbell et al., 1998). Owing to a lack of moisture and highly variable temperatures, the soils have relatively low biomass per unit area compared with lakes and streambeds of the MDV. The exception is the soils adjacent to streams and lakes which have higher biomass and activity than the surrounding soils (Hopkins et al., 2006; Ayres et al., 2007; Zeglin et al., 2009).

Wind plays an important role in the MDV in that it physically redistributes organic matter and soils (Lancaster, 2002; Nkem et al., 2006). For example, benthic microbial mats in the lakes lift off the bottom of the lakes, are conveyed through the ice cover and released at the surface where wind transports them throughout the valleys (Parker et al., 1982). Similarly, stream microbial mats may be dispersed by wind to new locations in the valleys. Additionally, winds are often strong enough to transport soil particles, which may be important in redistributing the microorganisms associated with them (Nkem et al., 2006). For example, sediment may be deposited by the wind on the surface of glaciers (Porazinska et al., 2004). Because the deposits have a higher albedo than the surrounding ice, they absorb more energy and create vertical melt holes called cryoconites. The debris seeds the cryoconites with

microorganisms and provides minute amounts of nutrients that enable biological activity. Biomass synthesized in cryoconites is eventually transferred down-valley during major melt events that flush melt holes out of the glacier and complete the cycle of biomass and energy transfer in the valleys (Wharton et al., 1985; Christner et al., 2003; Fountain et al., 2004; Porazinska et al., 2004; Foreman et al., 2007).

### **The McMurdo Dry Valley food web**

Biodiversity in the MDV is composed entirely of microinvertebrates including prokaryotes (Bacteria and Archaea), protists (phytoplankton and heterotrophic nanoflagellates), and invertebrates (Arthropoda, Tardigrada, Nematoda, and Rotifera). There are no extant vertebrate communities in the MDV (Adams et al., 2006). For many years, the food web of MDV lakes was characterized as relatively simple compared with more temperate ecosystems. This perception arose because the lakes were discovered to contain no crustaceans or fish. Biotic interactions such as predation were considered to be insignificant because protozoa were believed to be relatively sparse and the existence of viruses was unknown (Vincent and James, 1996). It is now clear that biotic interactions are much more complex than originally anticipated (Laybourn-Parry, 1997; Takacs and Priscu, 1998; Roberts et al., 2000) and, at least in the aquatic environment, viral lysis and predation have been detected (Kepner et al., 1998; Lisle and Priscu, 2004; S awstr om et al., 2008).

Nematodes, which feed on bacteria and algae, are at the top of the food chain and are represented by only five species (Adams et al., 2006). Tardigrades and rotifers are found in many of the MDV habitats, but have received little attention compared with the other groups of MDV inhabitants. Mosses are found in wetted areas of the terrestrial environment, for example along streams, near glaciers, and in depressions where snow may collect (Schwarz et al., 1992; Dale et al., 1999; Adams et al., 2006). Algae occur throughout the MDV, and as many as 40 unique diatoms have been identified in streams (Esposito et al., 2006). Protists and fungi are most abundant in the aquatic and the terrestrial habitats, respectively (Baublis et al., 1991; Kepner et al., 1999; Adams et al., 2006; Connell et al., 2006; Fell et al., 2006).

Diversity is much higher among the prokaryotes, or members of the Bacteria and Archaea. Bacteria exist throughout the valleys in the soils, lakes, streams, and even the lake and glacier ice (Adams et al., 2006) and include the cyanobacteria, which are the major primary producers in many of these systems. Bacteria have been studied in the MDV since the 1960s, but it is only recently that we have begun to appreciate the diversity of these

organisms (Gordon et al., 2000; Cowan and Tow, 2004; Stackebrandt et al., 2004; Barrett et al., 2006; Sattley and Madigan, 2006; Smith et al., 2006).

A major obstacle in studying microorganisms in nature has been methodology. Early studies of prokaryotic diversity relied to a large extent on enrichment cultures and isolating individual species. The first reports of MDV microbial diversity were of bacteria isolated from the lakes; only a handful of species were isolated, leading to a perception that bacteria were not very diverse or important in the MDV (Cameron et al., 1970; Horowitz et al., 1972; Friedmann, 1993). We now know that not all microorganisms are amenable to culturing, making this method highly selective and unrepresentative of actual biodiversity. It is estimated that less than 1% of organisms in the environment are directly cultivable using current techniques (Amann et al., 1995) and the cultivable organisms rarely represent the ecologically dominant members of the community (Ward, 1998). This is true of all environments, and perhaps more so for extreme environments where the isolation of organisms may require creative approaches to approximate the conditions under which life can thrive (Glausiuz, 2007; Stingl et al., 2008). Presently, the most effective means we have of assessing microbial diversity is by surveying community genomic DNA for phylogenetically important genes, such as the gene that codes for the small subunit of the ribosome (SSU rRNA genes or 16S and 18S rDNA in prokaryotes and eukaryotes, respectively), which allows us to make evolutionary comparisons among all domains of life.

Most of the recent prokaryotic microbial diversity assessments in the MDV have focused on the Bacteria and few reports of Archaea exist. The current understanding is that Archaea are not widespread in the MDV, but limited to anoxic or high salinity regions that harbor either methanogens or halophilic Archaea, respectively (Franzmann et al., 1997; Bowman et al., 2000; Brambilla et al., 2001). However, a more complete picture of microbial diversity in the MDV will develop as the region is sampled more extensively and alternative approaches such as environmental metagenomics are applied to the MDV. Given that the MDV environment is analogous to past and present conditions on Mars (McKay et al., 2005), we can use these observations to make inferences about the potential for life and its diversity on Mars.

## **Microbial biodiversity of MDV habitats**

### *Streams*

Streams within the MDV are ephemeral, with seasonal flow driven by solar radiation, geomorphology, and hyporheic exchange (Conovitz et al., 1998; Cozzetto et al., 2006). The annual flow period is on average six weeks, though

discharge is highly variable on annual and diel timescales. Streams in the MDV support high levels of biomass compared with the surrounding soils (McKnight et al., 1998), though much of this biomass is thought to be inactive or senescing (Vincent and Howard-Williams, 1989). Biodiversity studies of MDV streams have focused on the algal and cyanobacterial communities and no reports of nonphotosynthetic bacteria exist. Liquid water is present during the austral summer and autumn, which interacts with the sediments and soil, where C and N can be stored from year to year to supply organisms with essential nutrients and a medium for biosynthesis to occur (Runkel et al., 1998). Cyanobacterial mats and associated biota (Vincent, 1988; McKnight et al., 1999) in and along streams are centers of biological activity, including photosynthesis and nitrogen fixation by cyanobacteria, which is transferred to other organisms within the mat.

Given the paucity of grazing organisms in the MDV and the strong physical forcing of streams (e.g., highly variable flow, seasonal solar radiation, freeze–thaw), abiotic factors may be expected to structure microbial assemblages rather than biotic factors such as grazing and competition (Poff and Ward, 1989; Hogg et al., 2006). Geomorphic template and flow regime have been shown to control the distribution of photosynthetic mats in many MDV streams (McKnight et al., 1998, 1999; Esposito et al., 2006). For example, flow in streams with steep gradients is either too high or does not provide an adequate substrate for mat colonization. Mid-gradient reaches with stone pavement substrate support the highest densities of mat biomass. Dominant cyanobacterial species in stream mats vary spatially with flow regime. Mats dominated by *Nostoc* sp. generally line the edges of streams, while mats dominated by *Oscillatoria* sp. and *Phormidium* sp. occur in the middle of streams where flow rates are the highest (McKnight et al., 1998).

Cyanobacterial mats in MDV streams can survive freeze/thaw cycles and extended periods in a lyophilized state during the austral winter. They revive quickly upon exposure to liquid water during the austral summer (Vincent and Howard-Williams, 1986) and begin photosynthesizing in as little as 10 to 20 minutes after rehydration (Vincent and Howard-Williams, 1986). Furthermore, one week after restoring flow to a relict channel that had not received significant flow in approximately 20 years, the cyanobacterial mats became more abundant than in the surrounding streams due to increased solute concentrations in the reactivated stream channel. Cryptobiotic preservation of cyanobacterial mats enables MDV streams to respond rapidly to climatic and geomorphological change, similar to other arid zone stream ecosystems (McKnight et al., 2007).

### *Lakes*

The lakes of the MDV have varying degrees of chemical stratification and, in general, all contain nutrient-rich deep water covered by a relatively nutrient-poor trophogenic zone (Priscu, 1995; Dore and Priscu, 2001). The permanent ice cover of these lakes prevents wind-driven mixing, which coupled with low advective stream input allows vertical chemical and biological gradients to develop and persist (vertical mixing is at the molecular level throughout the water column, Spigel and Priscu, 1998). These physicochemical gradients provide a spectrum of diverse habitats that are represented by the unique microbial communities that inhabit them (Karr et al., 2003; Glatz et al., 2006; Sattley and Madigan, 2006; Clocksin et al., 2007).

The Taylor Valley lakes have received the most attention among lakes of the MDV. Lake Bonney is the most stratified of the lakes, followed by Lake Fryxell, and then Lake Hoare. Lake levels have fluctuated over the past 6000 years, effectively concentrating the solutes in the bottom waters of the lakes by evaporation and sublimation. An exception is Lake Hoare, which is believed to have dried out completely approximately 1200 years ago, whereas Lakes Fryxell and Bonney are believed to have persisted as ice-free brine ponds during the periods of low lake levels (Matsubaya et al., 1979; Lyons et al., 2004). Bottom-water dissolved inorganic carbon ages measured by  $^{14}\text{C}$  dating are approximately 1200 years in Lake Hoare and 8000 years in Lake Bonney (Doran et al., 1994). The  $^{14}\text{C}$  age of the fulvic acid fraction of Lake Fryxell's bottom waters has been determined to be approximately 3000 years (Aiken et al., 1996).

The lakes were discovered during Scott's exploration of the area in the early 1900s (Scott, 1905), but were not extensively studied until the 1960s when the first quantitative physical, chemical, and biological measurements were made (Armitage and House, 1962; Angino et al., 1964; Goldman, 1964; Goldman et al., 1967). However, a majority of these studies focused on the phytoplankton (Koob and Leister, 1972; Parker et al., 1977; Vincent, 1981; Lizotte et al., 1996). Of the studies that were concerned with the bacterioplankton, biomass and production were largely underestimated. Essentially all of these studies were conducted during a time when bacterial colony plate counts were the standard technique of determining bacterial abundance (Koob and Leister, 1972; Mikell et al., 1986).

The complexity and diversity of the lake microbial communities have only begun to be appreciated in the past decade (Laybourn-Parry, 1997; Ward and Priscu, 1997; Kepner et al., 1998; Takacs and Priscu, 1998; Priscu et al., 1999; Voytek et al., 1999; Roberts et al., 2000, 2004; Lisle and Priscu, 2004;

Mikucki and Priscu, 2007). Bacterial abundance and activity measurements revealed that bacteria play a significant role in carbon transformations in the lakes, and biomass losses indicated that grazing must be occurring (Takacs and Priscu, 1998). Seminal studies describing micro-eukaryote and viral populations expanded our understanding of the MDV lake food webs and provided evidence of an active microbial loop (Kepner et al., 1998; Priscu et al., 1999; Roberts and Laybourn-Parry, 1999; Roberts et al., 2000; Lisle and Priscu, 2004).

An extensive study of nitrogen dynamics in Lake Bonney revealed the importance of nitrification and denitrification in this system (Priscu, 1995; Priscu et al., 1996, 2002, 2008; Ward and Priscu, 1997; Voytek et al., 1999; Lee et al., 2004). A major focus of this research was on the high levels of nitrous oxide (>70 000% air saturation) and apparent lack of denitrification in the suboxic waters of the east lobe of the lake. A thermodynamic study of the biogeochemistry in MDV lakes indicates that present-day conditions in the east lobe of Lake Bonney are not favorable for contemporary formation of the nitrous oxide found there and that it is likely a vestige of some previous microbial community that existed when the redox conditions of the lake were more reducing (Lee et al., 2004). Another study based on metabolic genes and stable isotopes concluded that the gradients in nitrous oxide present in the lake today are relicts of ancient biogeochemical transformations, which owing to the 50 000-year mixing time of the lake, have yet to diffuse to equilibrium (Priscu et al., 2008).

Immunofluorescent probes specific for two denitrifying isolates from Lake Bonney revealed that potential denitrifiers were scarce in the deep waters of the east lobe, relative to the west lobe. Denitrification was proposed to be absent in the east lobe because of inhibition by salts, temperature, or possibly some other chemical limiting or inhibiting factor (Ward and Priscu, 1997). Denitrification could be induced in east lobe lake water that was diluted with ion-free water and incubated at temperatures higher than those *in situ* (Ward et al., 2005).

The importance of nitrifying bacteria in MDV lakes was determined by the development of a polymerase chain reaction (PCR) assay for the detection of ammonium oxidizers (Voytek and Ward, 1995; Voytek et al., 1999; Priscu et al., 2008). Ammonium oxidizers of the  $\beta$ -Proteobacteria were present in all lakes tested, whereas members of the  $\gamma$ -Proteobacteria, which is represented primarily by marine organisms, were detected in the saline Lakes Fryxell and Bonney, but not in Hoare (Voytek et al., 1999). Ammonium oxidizers were most abundant above the chemocline of the lakes and were associated with lower concentrations of ammonium and higher concentrations of nitrate and nitrite.



The microbial diversity of Lake Bonney's water column and ice cover has been assayed by SSU rRNA gene analysis (Gordon et al., 2000; Glatz et al., 2006). The sequences detected were unique among the depths sampled and many of the depths had little overlap in their communities. Diversity is low compared with other extreme aquatic habitats (Hughes et al., 2001), especially at the deepest depth surveyed, 25 m of Lake Bonney's east lobe, where temperatures and salinity are most limiting compared with the other depths sampled (Glatz et al., 2006).

A number of the phylotypes detected in Lake Bonney SSU rRNA gene analyses have now been cultured using a high throughput culturing method by amending filter sterilized lake water with additional carbon and nitrogen and inoculating media with lake water diluted to extinction (Stingl et al., 2008). This approach ensures that organisms that are most numerous in the water column serve as inoculum by diluting out any zymogenous or transient organisms and enriches the native organisms by providing media that closely resemble *in situ* conditions. Based on SSU rRNA gene analysis, 18 unique psychrotolerant bacterial cultures were isolated. In comparison with many standard culture studies, a majority of the isolates were not closely related to previously described bacterial species, and some of the cultures represent deeply branching members of their respective phyla (Stingl et al., 2008).

Lake Fryxell, a meromictic lake, is the most productive of the Taylor Valley lakes per unit volume (Takacs and Priscu, 1998). In a survey of the diversity of *pufM* genes, which encode for a pigment-binding protein in the photosynthetic reaction center of all purple phototrophic bacteria, no purple sulfur bacteria were detected; only purple nonsulfur bacteria were found (Karr et al., 2003), which was surprising given that Lake Fryxell has an active sulfur cycle. However, purple nonsulfur bacteria are metabolically more diverse than purple sulfur bacteria and are capable of chemoorganotrophic and chemolithotrophic growth in the dark. Thus, purple nonsulfur bacteria may maintain a competitive edge owing to the low light levels in Lake Fryxell (Karr et al., 2003).

Of the four groups of purple nonsulfur bacteria found in Lake Fryxell, only one was >90% identical in its *pufM* gene to previously cultured organisms. The four groups were detected in separate areas of the water column, distributed presumably according to oxygen, light, and sulfur concentrations indicating niche differentiation among the organisms represented by the sequences. One representative each from two of the four Lake Fryxell purple nonsulfur bacteria groups have been isolated. One of the isolates, *Rhodospirillum rubrum* (strain Fryx1), is the first member of the purple nonsulfur bacteria isolated to contain gas vesicles (Karr et al., 2003). A separate strain of

*R. antarcticus* has also been isolated from antarctic mat material (Madigan et al., 2000), but the mat strain does not have gas vesicles, indicating that strain Fryx1 is uniquely adapted to planktonic life within Lake Fryxell (Jung et al., 2004).

Many nonphotosynthetic sulfur bacteria have been identified in Lake Fryxell (Karr et al., 2005; Sattley and Madigan, 2006). The gradients of sulfide and oxygen provide an ideal environment for microorganisms capable of sulfur oxidation. Three strains related to *Thiobacillus thioparus* have been isolated from Lake Fryxell and this population of sulfur-oxidizing chemolithotrophs is most abundant at the oxycline of the lake where they are positioned perfectly to take advantage of ideal gradients of sulfide and oxygen (Sattley and Madigan, 2006). Sulfide is produced below the oxycline by sulfate-reducing bacteria belonging to seven groups of sequences representative of the *Desulfovibrio*, *Desulfonema*, *Desulfobulbus*, *Desulfomusa* ( $\delta$ -Proteobacteria), the *Desulfotomaculum* (Firmicutes), and two deeply branching groups, one of which could not be phylogenetically constrained. Nucleotide sequences from all of these sulfate-reducing bacteria were only distantly (63–77% identical) related to their closest relatives. Three of the Lake Fryxell sulfate-reducing bacterial groups were found throughout the water column, whereas the remainder were distinctly stratified (Sattley and Madigan, 2006).

Two major phyla of the Archaea, the Euryarchaeota and the Crenarchaeota, have been detected in Lake Fryxell (Karr et al., 2006). Methanogenic archaea were found only in the sediments where acetogens also have been cultured (Sattley and Madigan, 2007). Lake Fryxell acetogens and methanogens may be involved in syntrophic interspecies hydrogen transfer, which is known to occur in laboratory cultures, sludges, and the sediments of freshwater lakes (Jones and Simon, 1985). Acetogenesis, which can be endergonic under fermentative conditions, is thermodynamically favored by the utilization of  $H_2$  by methanogens. Because sulfate is low in Lake Fryxell sediments, sulfate reducers are incapable of competing with methanogens for  $H_2$ . The presence of methanotrophic archaea suggests that methane may serve as an electron donor for sulfate reducers above the sediments of Lake Fryxell (Karr et al., 2006). The Crenarchaeota sequences detected in Lake Fryxell group with Marine Benthic Group C and are presumed to represent oxygenic sulfide and thiosulfate oxidizing organisms (Karr et al., 2006).

The microbial community of Lake Hoare, which is the least stratified and productive lake of the Taylor Valley, has received little attention. Based on culture dependent studies, a diverse group of chemoorganotrophic bacteria belonging to the Actinobacteria and the  $\alpha$ -,  $\beta$ -, and  $\gamma$ -Proteobacteria have been isolated (Clocksin et al., 2007). Although all of the cultures could grow

at subzero temperatures, only one of the strains was a true psychrophile incapable of growth at temperatures greater than 20 °C. The lack of psychrophily by these and other MDV microbial isolates (Madigan et al., 2000; Jung et al., 2004; Sattley and Madigan, 2006; Stingl et al., 2008) relative to marine sediment isolates, which are more frequently psychrotolerant, suggests that MDV lake microorganisms have not fully adapted to the cold owing to the young age of the lakes (Clocksin et al., 2007).

A diverse assemblage of bacterial SSU rRNA gene sequences were detected in the sediments that exist within the ice cover of Lake Bonney (Gordon et al., 2000). Sediments are deposited on lake ice in the MDV by wind and represent a dynamic equilibrium between downward movement because of melt balanced with upward movement by sublimation of the ice cover (Priscu et al., 1998). Liquid water has been shown to exist in association with these sediments for up to 150 days during summer (Fritsen et al., 1998). The microbial assemblage is composed of cyanobacterial and heterotrophic bacteria that represent a complete consortium capable of organic carbon production and nutrient cycling (Paerl and Priscu, 1998; Priscu et al., 1998).

Microorganisms have also been discovered in the ice cover of Lake Vida (Fritsen and Priscu, 1998; Mosier et al., 2007), which lies in the Victoria Valley of the MDV. This lake is unique among MDV lakes because it is composed of a 19-m ice cover that has sealed off a cold (−10 °C) highly saline (~245‰) brine from the surrounding environment for approximately 2800 years (Doran et al., 2003). Polymerase chain reaction screening indicated that bacterial and eukaryal SSU rRNA genes were present at all depths of the ice cover tested, but no archaeal genes were detected (Mosier et al., 2007). Distinct communities were found at all depths; the nucleotide sequences detected in the upper ice are representative of organisms from soil and freshwater habitats and are believed to originate primarily from aeolian deposition and glacial meltwater, which is deposited on the ice surface annually. Although the brine was not sampled, evidence exists that the bottom depths of the ice result from the liquid water below the ice cover (Doran et al., 2003). Bacterial SSU rRNA gene sequences detected in this portion of the ice cover were most closely related to sequences that were predominantly (65% identical) of marine origin (Mosier et al., 2007).

Microbial mats exist in the littoral zone of the lakes and harbor a diversity of microorganisms dominated by cyanobacteria. Lake Fryxell microbial mats were estimated to contain up to 20 taxa using Fourier-transform infrared spectroscopy (Tindall et al., 2000). In a separate study, at least 133 unique SSU rRNA gene sequences of bacteria and archaea were identified in microbial mats of Lake Fryxell (Brambilla et al., 2001). Recent phylogenetic

analyses using genomic tools have shown that the cyanobacterial taxa in the MDV lake mats not only have higher diversity than expected but also revealed a number of putative endemic taxa (Brambilla et al., 2001; Van Trappen et al., 2002, 2004; Taton et al., 2003; Shivaji et al., 2005).

### Soils

Soils represent one of the harshest habitats within the MDV landscape, being extremely dry, low in organic matter and other nutrients, and subject to freeze–thaw action on a regular basis (Campbell et al., 1998). Though these conditions do not appear to be conducive to life, certain MDV soils support life in surprising abundance and diversity (Cowan et al., 2002). Various reports have been published recently detailing the bacterial diversity of MDV soils, which is orders of magnitude higher than eukaryotic diversity (which may be universally true for soils). For example, although only eight soil bacteria were cultured, 61 unique SSU rRNA gene types were identified among four soil types with varying pH, moisture, and level of human disturbance, and from largely separated sites around the MDV and the McMurdo area (Aislabie et al., 2006). Diversity among the four sites was greatest in the wetter soils, but was nearly two times lower than found in similarly arid, but temperate soils from Arizona (Dunbar et al., 1999). Bacterial communities in three of the sites were largely composed of a few dominant sequence types, which is contrary to the more even species distribution of most studied soils (Borneman and Triplett, 1997; Torsvik et al., 2002; Lozupone and Knight, 2007) and was interpreted to indicate that the dominant sequence types represent organisms that are highly adapted to *in situ* conditions (Aislabie et al., 2006). Communities from all four sites were composed of members from the Bacteroidetes, Actinobacteria, Proteobacteria, Deinococcus-Thermus, Acidobacteria, and Cyanobacteria bacterial divisions, but the dominant sequence types differed among the sites, indicating that there may be regional variations in the soil microbial communities. Additionally, many of the SSU rRNA gene sequences were only distantly related to previously reported sequences (88–95% identical), indicating that there may be an endemic MDV soil microbial community. In a similar study aimed at characterizing the bacterial communities associated with five different MDV soils, similarly diverse communities were discovered (Aislabie et al., 2008). The major distinction among the soils was that the less suitable habitats (i.e., lower nutrient and water availability) were composed of novel 16S rRNA gene sequence types assigned to uncultured and unrecognized genera, whereas the community in an ornithogenic soil

(high nutrients due to avian inputs) was dominated by well-characterized spore-forming bacteria.

A much higher level of diversity has been found in the wetted soils adjacent to MDV streams and lakes (parafluvial sediments), which have higher levels of organic matter and moisture relative to the surrounding soils (Hopkins et al., 2006). In a soil sample from the edge of the Onyx River (Wright Valley), 376 unique 16S rRNA gene sequence types were detected, but the survey was estimated to be only 53% complete (Zeglin, 2008). This level of diversity is similar to what has been found in the most diverse soils reported, such as from the Amazon rain forest and arid temperate regions (Borneman and Triplett, 1997; Fierer and Jackson, 2006). Overall, the Onyx River parafluvial sediment communities were similar to MDV soils at the phylum level, but contained a higher level of genus-level diversity.

The near-surface permafrost of the MDV, which occurs 10 to 25 cm below the surface soils of the valleys, contains only  $10^3$  to  $10^5$  bacterial cells  $g^{-1}$ . Although bacterial abundances are low relative to other antarctic habitats and arctic permafrost, these organisms have been shown to remain viable following melt despite the low ambient temperatures (Gilichinsky, 2007). Bacteria, algae, and fungi have been found in the MDV permafrost. For the bacteria there was little difference between the phyla found above ground in the surface soils and throughout the permafrost. Owing to the vast range of soil exposure times and age of permafrost, antarctic permafrost likely contains some of the oldest individuals on Earth. Martian permafrost may harbor similarly ancient organisms.

The Beacon Valley sandstones of the MDV can retain water internally for several days after wetting by snowmelt and provide a refugium for terrestrial life in the MDV (de la Torre et al., 2003). Cryptoendolithic microorganisms inhabit the near-surface pore spaces of light transparent exposed rocks and form complex communities that are classified as dominated either by lichens or cyanobacteria (Friedmann et al., 1988). A molecular comparison of the two cryptoendolithic community types detected 51 unique SSU rRNA gene sequences belonging to the Bacteria and Eukarya and no Archaea were detected. Only 12% of the nucleotide sequences were greater than 98% identical to known sequences. Despite the diversity of nucleotide sequences detected, the dominant communities were composed of only a few functional groups. The lichen community was dominated by an ascomycete (Fungi) and a green alga. The cyanobacterial community was dominated by a sequence that was most closely related to cyanobacterial sequences found throughout the MDV and grouped with *Phormidium* spp. Additionally, a *Deinococcus*-like sequence (only 90% identical) and an aerobic anoxygenic phototrophic

$\alpha$ -Proteobacteria sequence represented 26% and 31% of the sequences detected, respectively (de la Torre et al., 2003). Whereas the lichen community was composed of Bacteria and Eukarya, no eukaryote sequences were found in the cyanobacterial community.

### *Cryoconites*

Cryoconites are cylindrical melt holes that form on the ablation zone of glaciers worldwide (Wharton et al., 1985). As sediments are deposited on glaciers by wind, they are preferentially heated during the summer owing to their low albedo compared with the surrounding ice. A melt hole forms that contains the deposited sediments at the base and, during summer, liquid water. Antarctic cryoconites are unique in that they contain a thicker ice lid (up to 36 cm) than cryoconite holes from elsewhere. In the MDV, where cryoconite holes cover 4–6% of glacier surfaces, they range from 5 cm to 145 cm in diameter and 4 cm to 56 cm in depth (Fountain et al., 2004). With the formation of water, hole deepening is accelerated by albedo feedback. The water has a lower albedo than the surrounding ice, and the formation of water melts more ice (Wharton et al., 1985). Finally, as the hole becomes deeper, growth slows because less solar radiation reaches the sediment and a steady state is achieved with respect to depth as the amount of melt equals the ablation rate of the glacier surface. Liquid water may persist in the holes for 1–3 months during the summer and individual cryoconites can persist for several years to a decade. Eventually the holes are lost by either hydraulic washout or glacial calving (Fountain et al., 2004) distributing their contents to the surrounding stream, soil, and lake habitats.

Cryoconites have been recognized as biological hot spots in glacial ecosystems for decades (Wharton et al., 1985). In the MDV, these holes harbor a diverse and active community, and the presence of microorganisms appears to increase melt and cryoconite hole development. For example, experiments have shown that the depth of live holes is 10% deeper compared with killed controls. Wind-deposited sediments seed the holes with microorganisms and minerals that are leached into the meltwater and provide nutrients for growth (Wharton et al., 1985). Photosynthesis and nitrogen fixation by cyanobacteria and algae in the summer provide organic carbon and nitrogen and support a food web that is similar in composition to other MDV habitats. Bacteria, fungi, ciliates, rotifers, tardigrades, and nematodes have been detected by amplification of SSU rRNA genes (Christner et al., 2003). Similarities of the detected gene sequences indicated that the cryoconite consortia originated from the surrounding stream, sediment, and lake habitats

(Foreman et al., 2007). Enumeration of rotifers by microscopy suggests that they are more abundant than would be expected of an inactive community that was composed of cells simply deposited by wind (Porazinska et al., 2004). Additionally, bacterial biomass, abundance, and activity were always highest in the sediment of cryoconite holes, rather than the overlying water. The composition of the microbial consortia varied between the sediment and ice layer and among holes from different glaciers (Foreman et al., 2007). These differences point to the importance of sediments as sources of nutrients to the consortium. Based on the density of cryoconite holes on MDV glaciers, it has been suggested that in warm years, flushing could provide significant nutrient and organic carbon to the MDV (Foreman et al., 2007). Chemistry of cryoconite hole water relative to glacier ice suggests that this would influence the chemistry of the glacial melt-stream (Fountain et al., 2004; Barrett et al., 2007).

Another source of runoff from glaciers is the discharge that originates subglacially, such as Blood Falls on the terminus of the Taylor Glacier. The source of Blood Falls is believed to be remnant ancient water from a Pliocene warming event that resulted in ocean level rises that filled the Taylor Valley. When the water receded, a marine sea remained at the Taylor Glacier terminus that was covered during a subsequent expansion of the glacier's terminus (Mikucki, 2005). Blood Falls waters are saline, iron rich, and contain viable microorganisms that are active and diverse. Microbial community activity and diversity is low, but is comparable to similar polar systems, though the phylogenetic diversity of the organisms detected was broad (Mikucki and Priscu, 2007).

### **Ecological factors promoting diversity in the MDV**

Although the microbial diversity of all known MDV habitats has been described (Vishniac, 1993; Voytek and Ward, 1995; Gordon et al., 2000; Brambilla et al., 2001; Van Trappen et al., 2002; de la Torre et al., 2003; Karr et al., 2003, 2005; Stackebrandt et al., 2004; Adams et al., 2006; Barrett et al., 2006; Glatz et al., 2006; Aislabie et al., 2008; Mikucki and Priscu, 2007; Sattley and Madigan, 2007; Stingl et al., 2008; Zeglin, 2008), very few of these reports explain the factors that contribute to the observed distribution and diversity (but see de la Torre et al., 2003; Karr et al., 2003, 2005, 2006; Glatz et al., 2006; Mikucki and Priscu, 2007; Aislabie et al., 2008) and a broad understanding of the factors structuring MDV microbial diversity is lacking. Here we synthesize published MDV bacterial 16S rRNA gene sequence data as a basis for inferring the processes that contribute to the microbial diversity patterns that have been observed in the MDV.

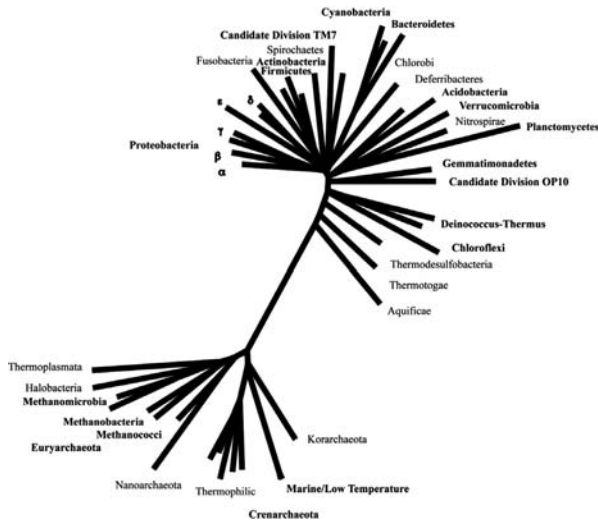


Fig. 8.2. Phylogenetic tree of the Bacteria and Archaea. Phyla for which sequences from the MDV have been retrieved are shown in bold. In addition to the phyla shown, many MDV sequences group with uncultured environmental sequences of unknown phylogeny or candidate divisions, such as TM7 and OP10 (shown) or OD1 and BD.

Surveys of SSU rRNA genes in MDV habitats indicate a broad taxonomic diversity among the bacteria, sequences group with over 15 bacterial phyla (Fig. 8.2) and revealed more diversity than observed among MDV eukaryotes (Brambilla et al., 2001; Smith et al., 2006; Stingl et al., 2008). A simple species richness estimator, such as the proportion of unique sequences (or operational taxonomic units, OTUs) detected per sample, enables comparison of 16S rRNA gene sequence richness from MDV habitats (Fig. 8.3). A similar level of richness was detected among the soil samples (Aislabie et al., 2006, 2008), a Lake Fryxell sample (C. Takacs-Vesbach et al., unpublished data), and from wetted sediments surrounding MDV streams (C. Takacs-Vesbach et al., unpublished data). A recent meta-analysis of over 21 000 16S rRNA gene sequences from diverse habitats worldwide concluded that microbial diversity is highest in sediments (Lozupone and Knight, 2007). Richness in the MDV is lowest in the icy habitats, such as cryoconites (Christner et al., 2003), lake ice (Gordon et al., 2000), and the outflow of Blood Falls (Mikucki and Priscu, 2007). Unfortunately, no SSU rRNA gene sequence data for MDV streams have been published (only algal diversity has been reported, e.g., Esposito et al., 2006).

Here we compare MDV bacterial richness with two similar studies conducted on Crater Lake, Oregon (Urbach et al., 2001, 2007) and soil from the Amazon rain forest (Borneman and Triplett, 1997; Urbach et al., 2001, 2007), and a microbial inventory of Yellowstone thermal features (C. Takacs-Vesbach,



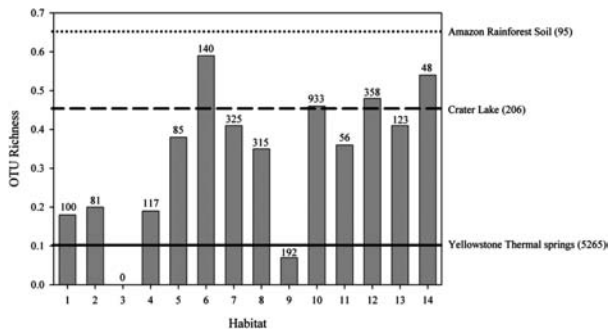


Fig. 8.3. Richness (proportion of unique bacterial sequences in a survey) of MDV habitats. 1, Cryoconite (Christner, 2003); 2, Blood Falls (Mikucki and Priscu, 2007); 3, streams (no data); 4, east lobe Lake Bonney (Glatz et al., 2006); 5, west lobe Lake Bonney (Glatz et al., 2006); 6, Lake Fryxell (C. Takacs-Vesbach, unpublished); 7, Lake Fryxell mat (Brambilla et al., 2001, Taton et al., 2003); 8, Lake Vida (Mosier et al., 2007); 9, Lake Bonney ice (Gordon et al., 2000); 10, wetted sediments along stream margins (C. Takacs-Vesbach, unpublished); 11, soils from Miers Valley (Aislabie et al., 2007); 12, soils from Wright Valley (Aislabie et al., 2006); 13, lichen dominated cryptoendolith (de la Torre et al., 2003); 14, cyanobacterial dominated cryptoendolith (de la Torre et al., 2003). Numbers above each bar represent the number of sequences surveyed in each study. Horizontal lines represent richness detected in a survey of 100 Yellowstone thermal springs (Takacs-Vesbach, unpublished), Crater Lake (Urbach et al., 2001, 2007), and an Amazon rain forest soil (Borneman and Triplett, 1997). Numbers in parentheses represent the total number of sequences screened in each study.

unpublished data). Crater Lake and the Amazonian soil were reported to have remarkably high levels of microbial diversity and MDV richness is lower, but higher than found in a survey of Yellowstone thermal features, which tend to be dominated by many closely related sequences from only a few genera (Hall et al., 2008; Takacs-Vesbach et al., 2008). Richness was used to compare all of these studies because robust diversity estimators were not reported in all of the studies, some of the studies did not completely survey their sequence libraries, and some reports did not include the number of sequences screened. However, comparison of the more complete data sets revealed that the amount of diversity detected among the sites was similar to the richness results, except that there were several individual sites – for example, sediments along the margins of Taylor Valley streams – which are expected to be as diverse as the Amazon soil sample, based on rarefaction, a more robust diversity estimator (Fig. 8.4).

Three characteristics of MDV diversity that are common among the existing bacterial SSU rRNA gene sequence data are (1) the nature of the abundance of unique SSU rRNA gene sequences, (2) the phylogenetic breadth of the communities, and (3) the novelty of the sequences. In almost all reports of

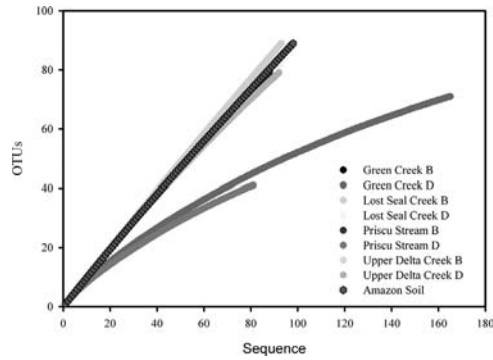


Fig. 8.4. Rarefaction curves of bacterial 16S rRNA gene libraries from margin sediments of MDV streams and an Amazon rain forest soil (Borneman and Triplett, 1997).

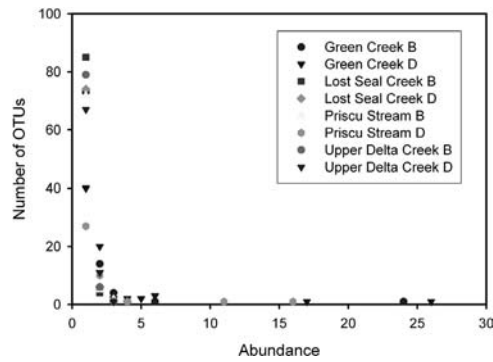


Fig. 8.5. Species abundance curves of the bacterial diversity detected in the wetted sediments found along the margins of Taylor Valley streams (C. Takacs-Vesbach, unpublished). A large proportion of the sequences were unique (<97% identical) and only a few sequences comprised more than five representatives. This type of diversity pattern, described as log series, is common among all the MDV habitats surveyed.

MDV microbial diversity, the SSU rRNA gene libraries are composed of few dominant sequences and a larger proportion of unique sequences that are represented by only one or a few clones (e.g., Brambilla et al., 2001; Mikucki and Priscu, 2007; Aislabie et al., 2008, and see Fig. 8.5). Communities defined by this type of richness abundance pattern are common among all domains of life and similar patterns of diversity have been found by a number of studies in varied MDV and other cold habitats (reviewed in Nemergut et al., 2005). The log series model of species diversity is used to describe communities with a high abundance of rare species and an ecological explanation for this type of diversity distribution is that one or a few factors determine the community assemblage (May, 1975; Magurran, 2004; Mikucki and Priscu, 2007).

Table 8.1. *Phylogenetic breadth of the bacterial sequences detected in MDV habitats*

Habitat	Average branch length <sup>a</sup>
Cryoconite	0.51
Blood Falls	0.36
East lobe Lake Bonney	0.41
Lake Bonney isolates	0.34
West lobe Lake Bonney	0.59
Lake Fryxell	0.64
Lake Fryxell isolates	0.30
Lake Fryxell mat	0.38
Lake Hoare isolates	0.48
Lake Vida	0.39
Lake Bonney Iice	0.48
Stream margins	0.37
Soils	0.38
Cryptoendolith	0.43

Notes: <sup>a</sup> Average branch length calculated as the sum of branch lengths for distance trees constructed for each habitat divided by the number of sequences in the tree (Lozupone and Knight, 2007).

Although species richness may be low in many of the MDV habitats, the phylogenetic breadth of all the communities is notable. A broad phylogenetic swath of microbial diversity is represented in the MDV (e.g., see Fig. 8.2), including sequences and isolates from the Chloroflexi, Deinococcus, Gemmatimonadetes, Planctomyces, Verrucomicrobia, Acidobacteria, Bacteroidetes, Cyanobacteria, Firmicutes and Actinobacteria, and Proteobacteria. Comparison of the average branch length of simple distance trees (Lozupone and Knight, 2007) constructed with the individual data sets reveals that phylogenetic breadth of the sites is similar (Table 8.1), but highest in Lake Fryxell and west Lake Bonney. Finally, many of the sequences detected in the MDV are less than 97% identical (some are as low as 60%) to other known sequences, indicating that MDV microorganisms are novel and may represent species unique to Antarctica.

Principal coordinate analysis (Lozupone and Knight, 2005) of MDV bacterial SSU rRNA gene sequences revealed that a number of the data sets cluster together based on habitat (Fig. 8.6). The bacterial isolates from Lakes Fryxell, Hoare, and Bonney all cluster with the ice habitats. The similarity between uncultured and cultured sea ice microorganisms has been noted before and related to the high success rate of culturing these bacteria (Lozupone and Knight, 2007). Central to the isolate and ice cluster are the soil sequences, which suggests an aeolian origin for the sequences that comprise these

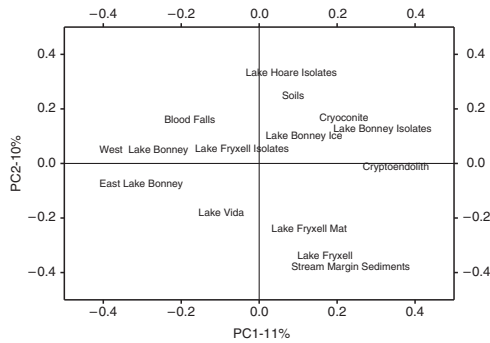


Fig. 8.6. Ordination of bacterial 16S rRNA gene sequences by MDV habitats: cryoconite (Christner et al., 2003); Blood Falls (Mikucki and Priscu, 2007); Lake Bonney (Glatz et al., 2006); Lake Fryxell, Lake Fryxell mat (Brambilla et al., 2001; Taton et al., 2003); Lake Vida (Mosier et al., 2007); Lake Bonney ice (Gordon et al., 2000); soils from Miers and Wright Valleys (Aislabie et al., 2006, 2007); cryptoendolith (de la Torre et al., 2003). Data were aligned using the Greengenes aligner (DeSantis et al., 2006) and analyzed by principal coordinate analysis in Unifrac (Lozupone and Knight, 2005).

habitats. A clear separation among the lake habitats exists, though the two lobes of Lake Bonney are clustered together, as are the Lake Fryxell mat and water column sequences. The sequences from MDV wetted sediments also grouped with Lake Fryxell. In the absence of any obvious similarities between these two habitats, the only explanation that can be provided is that the two habitats share some unidentified environmental factor that correlates with the first axis of the analysis. The cryptoendolithic community was the most divergent data set among the habitats.

That the microbial diversity of MDV habitats shares many patterns of community composition is suggestive that a unifying theme of community assemblage must be at work. However, unlike plant and animal diversity, a comprehensive framework for explaining microbial diversity is largely lacking (Torsvik et al., 2002; Horner-Devine et al., 2003, 2007; Lozupone and Knight, 2007). Because microorganisms and macroorganisms share the same fundamental biology, much of what we already know about plants and animals should also apply to microorganisms. Here we apply ecological explanations developed for eukaryotes to develop a hypothesis that explains the processes promoting microbial diversity in the MDV.

### *Spatial heterogeneity*

In general, species diversity is often higher in communities that inhabit more complex and heterogeneous physical environments (Zhou et al., 2002;

Torsvik et al., 2002; Lozupone and Knight, 2007), because greater spatial heterogeneity contributes to more potential niches (Roth, 1976; Huston, 1979). Spatial heterogeneity occurs over a number of scales in the MDV (Virginia and Wall, 1999). At the regional scale, geographical features (elevation, slopes, and aspect) contribute to differences in microclimate (Dana et al., 1998), while geological variation in soil parent material, mineralogy, and surface exposure age influence nutrient availability in soils, streams, and lakes (Lyons et al., 2004; Barrett et al., 2007; Bate et al., 2007). At meter to kilometer scales, variation in microbial communities (composition and diversity) is influenced by the dominant landforms: glaciers, ephemeral streams, sediments and soils, and lakes. Within each habitat type, we also see differences in biodiversity at finer scales (e.g., micrometer to meter). For example, a synoptic sampling of the soils surrounding the three major lakes of the Taylor Valley, Lakes Fryxell, Hoare, and Bonney, showed that there was a decrease in organic carbon and nitrogen content from east to west, with highest organic matter concentrations in the Fryxell basin and the lowest found in the Bonney basin (Fritsen et al., 2000). These differences in organic matter content broadly correspond to differences in till provenance, surface exposure age, and habitat suitability (Virginia and Wall, 1999; Barrett et al., 2004, 2007; Bate et al., 2007). Spatial heterogeneity in Taylor Valley soils is also hypothesized to affect the distribution of microbial biomass across the valley landscape, which is supported by an assessment of microbial enzymatic potential conducted on MDV soils that revealed similar basin level differences (Zeglin et al., 2009).

On the local scale, within the soils and lakes, gradients of major biotic determinants such as moisture, nutrients, and salt promote diversity because they offer a spectrum of habitat suitability. The water columns of the MDV lakes are hydraulically stable because the permanent ice covers and strong chemical gradients prevent wind-driven mixing (Spigel and Priscu, 1998). The resultant water layers provide a spectrum of microbial habitats. Distinct communities are found at different depths within Lake Fryxell (Fig. 8.7). Likewise, gradients of moisture, salinity, and nutrients in the soils adjacent to streams and lakes are accompanied by changes in community composition within the top 10 cm of sediments (Fig. 8.8).

On the microscale, microhabitats within aquatic systems and on individual grains of soil result from the patchiness found at this scale. For example, in aquatic systems, patches of higher nutrients are hypothesized to occur near a single phytoplankter because of cell exudates (Bell and Mitchell, 1972; Krembs et al., 1998). By clustering around such cells, chemotactic microorganisms capable of attachment have access to elevated nutrient levels

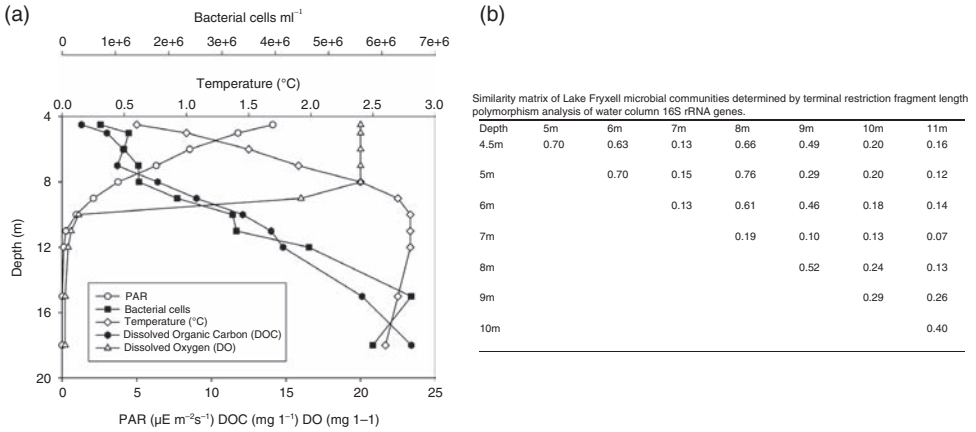


Fig. 8.7. Gradients in Lake Fryxell. (a) Physical, chemical, and biological profiles of Lake Fryxell water column. (b) similarity matrix of Lake Fryxell bacterial communities determined by terminal restriction fragment length polymorphisms of community 16S rRNA genes (C. Takacs-Vesbach, unpublished).

associated with biogeochemical transformations within the aggregate. MDV lakes are high in particulate organic matter where microbial abundance and biogeochemical cycling are elevated (Lisle and Priscu, 2004).

Sediments and soils are heterogeneous on the microscale as well. Steep chemical and physical gradients that affect nutrient concentration, redox conditions, and water availability create a large number of microscale habitats (Young and Ritz, 2000; Torsvik et al., 2002). These microhabitats provide distinct niches, spatially isolating microbial populations and result in a more complex microbial community (Zhou et al., 2002). In the MDV, sediments are biological hot spots in melt holes such as cryoconites and within the lake ice where bacteria and algae are concentrated (Priscu et al., 1998). The sediments contribute to the existence of liquid water and provide increased nutrient concentrations that support a higher abundance of life compared with the surrounding ice. The microbial diversity associated with ice sediments is similar to soil microbial diversity (Gordon et al., 2000) as illustrated in Fig. 8.5, which suggests that ice microbial communities are transplanted by wind, but are capable of growth when liquid water exists (Foreman et al., 2007). Given the wide range of habitat diversity present in the MDV and that microbial activity is detected throughout these habitats, it is not surprising that such a wide range of bacterial sequences have been detected (Voytek and Ward, 1995; Gordon et al., 2000; Madigan et al., 2000; Brambilla et al., 2001; Cowan et al., 2002; de la Torre et al., 2003; Karr et al., 2003, 2005, 2006; Taton et al., 2003; Barrett et al., 2004; Lisle and Priscu, 2004;

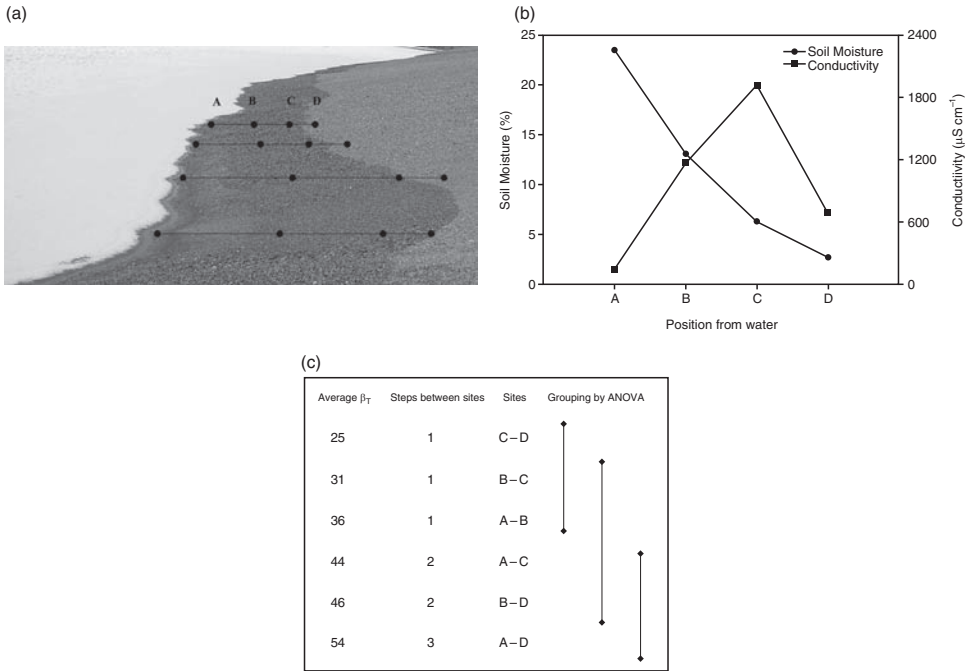


Fig. 8.8. Spatial heterogeneity of wetted sediments at the hydrologic margins of MDV lakes and streams. (a) Example of the wetted sediments that are clearly visible along MDV lakes and streams in summer. (b) A gradient of moisture and conductivity along the hydrologic margin habitat provides a spectrum of habitable niches. (c) Species turnover (beta diversity) along the wetted margins of Green Creek and Lake Fryxell. Community turnover metric  $\beta_T$  is lowest at 1-step distances between samples; turnover between the two outer sites (C–D) is lowest; the 3-step turnover is highest. Community turnover was determined by using the equation:  $\beta_T = (\text{change in number of sequences between two sites}/2) * \text{average community richness}$ .

Porazinska et al., 2004; Adams et al., 2006; Aislabie et al., 2006, 2008; Glatz et al., 2006; Smith et al., 2006; Mikucki and Priscu, 2007; Mosier et al., 2007; Stingl et al., 2008).

**Competition and predation**

Interspecific competition is widely believed to be a key determinant of biodiversity for plants and animals, although contradictory hypotheses exist. The competitive exclusion principle holds that if one competitor is more effective than another, it will eventually overcome the other species (Hardin, 1960). A major criticism of competitive exclusion is the assumption of

equilibrium conditions, which are rarely achieved in nature (Huston, 1979). However, even in the absence of equilibrium, it might be expected that the immediate outcome of competition would be the dominance of one competitor over another and that intense competition should result in low diversity among competing species (Levins, 1968). Alternatively, competition may increase diversity because it favors reduced niche breadth and, therefore, more potential niches or coexisting species (May, 1974; Schoener, 1974).

Laboratory experiments of model aquatic microbial communities indicate that competition drives community structure (Tilman et al., 1982; Sommer, 1985), but for more complex communities such as those found in soils, this does not seem to hold. For example, the microbial diversity of heterogeneous versus homogeneous soils under limiting nutrient conditions was investigated by comparing bacterial communities in dry and saturated soils containing low organic carbon. Bacterial diversity was lower in the more homogeneous soil indicating that competitive exclusion was occurring because the species evenness was lower in the saturated soil community compared with the unsaturated soils (Zhou et al., 2002).

Soil moisture is very low in the MDV. Approximately 95% of the landscape is not moistened by liquid water although soil may be intermittently wetted for short periods by snowfall (Campbell et al., 1998). Adjacent to more consistent water sources such as streams and lakes, the moisture content of valley soils/sediments is only 15%. Decreased competition because of spatial separation owing to low moisture can contribute to the diversity observed in MDV soils (Cowan et al., 2002; Connell et al., 2006; Smith et al., 2006). Furthermore, the low growth rates that have been reported from all MDV habitats (Kepner et al., 1998; Priscu et al., 1998; Takacs and Priscu, 1998; Roberts et al., 2000; Foreman et al., 2007; Mikucki and Priscu, 2007; Zeglin et al., 2009) can decrease competitive interactions. An alternative hypothesis of competitive equilibrium focuses on the rate of competitive displacement (Huston, 1979) by comparing the rates at which differences in competitive abilities are expressed. If all competing species are increasing at a very low rate, the better competitor will be slow to predominate. Under fluctuating environmental conditions, competitive equilibrium is not reached and diversity is strongly influenced by the rate of competitive displacement (Huston, 1979). Under conditions where the rate of competitive displacement is low, species evenness will be high and individual species will occur at low density, which is consistent with the patterns of microbial diversity observed in the MDV (see Fig. 8.4). Therefore, spatial and temporal separation of microbial interactions in the MDV likely contributes to the apparent high microbial diversity.



Predation can be important in determining biodiversity in communities with many interactions among members of the food web. Predation is believed to increase biodiversity by maintaining low abundances of individual species, thus reducing competition (Paine, 1966). This is especially true in the tropics where there are many biotic interactions among populations, and has been shown experimentally and theoretically in the seminal works of Connell (1961) and Gause (1934). Historically, predation was not believed to be important in the MDV ecosystem (Vincent and James, 1996; Hogg et al., 2006). However, it is now clear that potential grazers and viruses are abundant in the lakes and bacterial abundances are known to decrease by up to 88% during the summer (Takacs and Priscu, 1998; Lisle and Priscu, 2004). These biotic interactions potentially affect microbial abundance and diversity in the MDV lakes, but less is known about the soils. Nematodes are the major grazers in MDV soils (Treonis et al., 1999), but no relationship between nematode abundances and microbial diversity is apparent in the studies that examined multitrophic relationships (Barrett et al., 2006; Niederberger et al., 2008).

### *Temporal variability and disturbance*

An intermediate level of disturbance maintains spatial and temporal heterogeneity in habitat type and resource availability, and is thus correlated with a high level of diversity (Connell, 1978). This phenomenon is evident in stream ecosystems, which are dynamic by nature (Townsend et al., 1997). In MDV streams, the highest levels of diatom diversity and endemism are found at moderate flow regime harshness (i.e., length and intensity of stream discharge events, Esposito et al., 2006). Further, some views hold that harsh conditions, periodic disturbances, or resource pulses can promote species coexistence by preventing competitive equilibrium and allowing greater niche overlap (Hutchinson, 1961), while others maintain that harsh, unpredictable conditions drive the evolution of temporally staggered competitive strategies that maintain diversity (Chesson and Huntly, 1997; Chesson et al., 2004). A recent evaluation of factors governing soil invertebrate distribution across the MDV landscape invoked the presence of harshness-tolerant strategies as maintaining regional diversity (Bamforth et al., 2005). Another recent study showed that meltwater pulses occurring during an extreme climate event in the MDV stimulated the abundance and activity of a subordinate soil invertebrate species, and thus may contribute to the maintenance of soil biodiversity (Barrett et al., 2008).

If the lack of competitive displacement explains the persistence of MDV diversity, then how is microbial diversity generated in the MDV? Among

naturally occurring populations, there are two opposing forces governing community composition: genetic divergence among populations, and disturbances that purge poorly adapted subpopulations (Thompson et al., 2005). Divergence occurs through genetic mutations that can accumulate and persist because they are neutral or favored by selection (Ward et al., 2008). Although bacterial growth is limited to only a few weeks each year in many MDV habitats, which would limit speciation, the potential exists for heightened mutagenesis due to increased UV at the poles, as has been observed in antarctic mosses (Skotnicki et al., 2000). Despite the broad phylogenetic breadth of microbial sequences detected in the MDV, a striking feature is that within MDV phyla, there are many unique, but closely related 16S rRNA gene sequences (Christner et al., 2003; Karr et al., 2003, 2005; Aislabie et al., 2006, 2008; Glatz et al., 2006). In a survey of bacterial diversity associated with soils collected along the margin of the Onyx River (Wright Valley), 16% of the unique sequences (defined as <97% identical) grouped within a single genus of the Bacteroidetes (*Niastella*, Family Flexibacter) (Zeglin, 2008). This variation may represent accumulated neutral mutations (Thompson et al., 2005) or the persistence of closely related species adapted to different niches (Lozupone and Knight, 2007; Ward et al., 2008).

Disturbances capable of purging genetic variation occur over various timescales in the MDV: for example, the highly variable stream hydrograph in summer (hours to days, Conovitz et al., 1998), the diphotic cycle (months), and cooling and warming trends that may last on the order of decades to millennia (Doran et al., 2002). However, these disturbances presumably are rarely catastrophic and because decomposition rates are so low (Takacs and Priscu, 1998; Priscu et al., 1999; Takacs et al., 2001; Zeglin et al., 2009), any diversity that is generated in the MDV can persist in the environment and be detected by modern molecular diversity assessments.

## Conclusions

Although a considerable amount of work has focused on microbial activity and function of the MDV ecosystem, our understanding of microbial biodiversity in this unique environment remains incomplete. However, there are notable similarities regarding the bacterial diversity among MDV habitats that are also characteristic of other cold environments (Nemergut et al., 2005). The varied landscape of the MDV provides a spectrum of habitats that support a broad bacterial richness. We hypothesize that similar to other microbial populations worldwide, diversity is generated by the accumulation of mutations (neutral and adaptive) that persist in the environment because disturbance is rarely

catastrophic for these slow-growing populations. At the same time, low bacterial growth rates result in a community where competitive displacement is infrequent.

Physical conditions on Mars have been cold, and in some habitats arid, for at least 3 billion years. Therefore, many contemporary MDV habitats may share similarities with conditions on Mars. Water on Mars must be frozen and solar heating of the subsurface of the ice that covers the planet may result in liquid inclusions similar to lake ice and cryoconites, which could serve as refugia for microorganisms in the hostile glacial surface environment, and may have analogs in the polar ice caps of Mars (Wharton et al., 1985). Antarctic permafrost is of significance because although these organisms are believed to be dormant, if Mars was inhabited in the past, then remnants of this life might be found entrained in Mars permafrost as well. Inspection by electron microscopy of cells defrosted from antarctic permafrost revealed that the cells were largely intact. Indeed, because many cultures have been isolated from the permafrost, this would suggest that perhaps some primitive life may some day be isolated from martian permafrost (Gilichinsky, 2007). Cryptoendolithic communities would be ideally suited to the low water, high ionizing conditions found on Mars. Presumably, life there would have been (or is presently) subjected to similar environmental pressures that would limit biotic interactions and produce similar patterns of microbial diversity.

Examination of the nature of MDV diversity, overwhelmed by rare and divergent sequences, indicates that this is a resource of tremendous genomic potential that may prove to be of applied and medical importance. It will be important in the future to achieve a thorough understanding of this diversity, and the factors promoting and limiting it, because it will provide us with major insights into fundamental ecological processes in the MDV, on Earth, and potentially other planets with similar ecological conditions.

## References

- Adams, B. J., Bardgett, R. D., Ayres, E., et al. (2006). Diversity and distribution of Victoria Land biota. *Soil Biology and Biochemistry*, **38**, 3003–3018.
- Adams, E. E., Priscu, J. C., Fritsen, C. H., Smith, S. R., and Brackman, S. L. (1998). Permanent ice covers of the McMurdo Dry Valley lakes, Antarctica: bubble formation and metamorphism. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Priscu. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 281–296.
- Aiken, G., McKnight, D., Harnish, R., and Wershaw, R. (1996). Geochemistry of aquatic humic substances in the Lake Fryxell Basin, Antarctica. *Biogeochemistry*, **34**, 157–188.
- Aislabie, J. M., Chhour, K. L., Saul, D. J., et al. (2006). Dominant bacteria in soils of Marble Point and Wright Valley, Victoria Land, Antarctica. *Soil Biology and Biochemistry*, **38**, 3041–3056.

- Aislabie, J. M., Jordan, S., and Barker, G. M. (2008). Relation between soil classification and bacterial diversity in soils of the Ross Sea region, Antarctica. *Geoderma*, **144**, 9–20.
- Amann, R. I., Ludwig, W., and Schleifer, K.-H. (1995). Phylogenetic identification and in situ detection of individual microbial cells without cultivation. *Microbiological Reviews*, **59**, 143–169.
- Angino, E. E., Armitage, K. B., and Tash, J. C. (1964). Physicochemical limnology of Lake Bonney, Antarctica. *Limnology and Oceanography*, **9**, 207–217.
- Armitage, K. B. and House, H. B. (1962). A limnological reconnaissance in the area of McMurdo Sound, Antarctica. *Limnology and Oceanography*, **7**, 36–41.
- Ayres, E. B., Adams, B. J., Barrett, J. E., Virginia, R. A., and Wall, D. H. (2007). Unique similarity of faunal communities across aquatic-terrestrial interfaces in a polar desert ecosystem: soil-sediment boundaries and faunal community. *Ecosystems*, **10**, 523–535.
- Bamforth, S. S., Wall, D. H., and Virginia, R. A. (2005). Distribution and diversity of soil protozoa in the McMurdo Dry Valleys of Antarctica. *Polar Biology*, **28**, 756–762.
- Barrett, J. E., Virginia, R. A., Wall, D. H., et al. (2004). Variation in biogeochemistry and soil biodiversity across spatial scales in a polar desert ecosystem. *Ecology*, **85**, 3105–3118.
- Barrett, J. E., Virginia, R. A., Wall, D. H., et al. (2006). Co-variation in soil biodiversity and biogeochemistry in northern and southern Victoria Land, Antarctica. *Antarctic Science*, **18**, 535–548.
- Barrett, J. E., Virginia, R. A., Lyons, W. B., et al. (2007). Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. *Journal of Geophysical Research*, **112**, G01010.
- Barrett, J. E., Virginia, R. A., Wall, D. H., et al. (2008). Persistent effects of a discrete climate event on a polar desert ecosystem. *Global Change Biology*, doi: 10.1111/j.1365-2486.2008.01641.x.
- Bate, D. B., Barrett, J. E., Poage, M. A., and Virginia, R. A. (2007). Soil phosphorus cycling in an Antarctic polar desert. *Geoderma*, **144**, 21–31.
- Baublis, J. A., Wharton, R. A., and Volz, P. A. (1991). Diversity of micro-fungi in an Antarctic dry valley. *Journal of Basic Microbiology*, **31**, 3–12.
- Bell, W. and Mitchell, R. (1972). Chemotactic and growth responses of marine bacteria to extracellular products. *Biological Bulletin*, **143**, 265.
- Borneman, J. and Triplett, E. W. (1997). Molecular microbial diversity in soils from eastern Amazonia: evidence for unusual microorganisms and microbial population shifts associated with deforestation. *Applied and Environmental Microbiology*, **63**, 2647–2653.
- Bowman, J. P., McCammon, S. A., Rea, S. M., and McMeekin, T. A. (2000). The microbial composition of three limnologically disparate hypersaline Antarctic lakes. *FEMS Microbiology Letters*, **183**, 81–88.
- Brambilla, E., Hippe, H., Hagelstein, A., Tindall, B. J., and Stackebrandt, E. (2001). 16S rDNA diversity of cultured and uncultured prokaryotes of a mat sample from Lake Fryxell, McMurdo Dry Valleys, Antarctica. *Extremophiles*, **5**, 23–33.
- Burkins, M. B., Virginia, R. A., and Wall, D. H. (2001). Organic carbon cycling in Taylor Valley, Antarctica: quantifying soil reservoirs and soil respiration. *Global Change Biology*, **7**, 113–125.
- Cameron, R. E., King, J., and David, C. N. (1970). Soil microbial ecology of Wheeler Valley, Antarctica. *Soil Science*, **109**, 110–120.

- Campbell, I. B., Claridge, G. G., Campbell, D. I., and Balks, M. R. (1998). The soil environment of the McMurdo Dry Valleys, Antarctica. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Prisco. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 297–322.
- Chesson, P. and Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, **150**, 519–553.
- Chesson, P., Gebauer, R. L. E., Schwinning, S., et al. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, **141**, 236–253.
- Christner, B. C., Kvitko, 2nd, B. H., and Reeve, J. N. (2003). Molecular identification of bacteria and eukarya inhabiting an Antarctic cryoconite hole. *Extremophiles*, **7**, 177–183.
- Clocksins, K. M., Jung, D. O., and Madigan, M. T. (2007). Cold-active chemoorganotrophic bacteria from permanently ice-covered Lake Hoare, McMurdo Dry Valleys, Antarctica. *Applied and Environmental Microbiology*, **73**, 3077–3083.
- Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**, 710–723.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. *Science*, **199**, 1302–1310.
- Connell, L., Redman, R., Craig, S., and Rodriguez, R. (2006). Distribution and abundance of fungi in the soils of Taylor Valley, Antarctica. *Soil Biology and Biochemistry*, **38**, 3083–3094.
- Conovitz, P. A., McKnight, D. M., MacDonald, L. H., Fountain, A. G., and House, H. R. (1998). Hydrological processes influencing streamflow variation in Fryxell Basin, Antarctica. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Prisco. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 93–108.
- Cowan, D. A. and Tow, L. A. (2004). Endangered Antarctic environments. *Annual Review of Microbiology*, **58**, 649–690.
- Cowan, D. A., Russell, N. J., Mamais, A., and Sheppard, D. M. (2002). Antarctic dry valley mineral soils contain unexpectedly high levels of microbial biomass. *Extremophiles*, **6**, 431–436.
- Cozzetto, K., McKnight, D., Nylén, T., and Fountain, A. (2006). Experimental investigations into processes controlling stream and hyporheic temperatures, Fryxell Basin, Antarctica. *Advances in Water Resources*, **29**, 130–153.
- Dale, T. M., Skotnicki, M. L., Adam, K. D., and Selkirk, P. M. (1999). Genetic diversity in the moss *Hennediella heimii* in Miers Valley, southern Victoria Land, Antarctica. *Polar Biology*, **21**, 228–233.
- Dana, G. L., Wharton, Jr., R. A., and Dubayah, R. (1998). Solar radiation in the McMurdo Dry Valleys, Antarctica. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Prisco. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 39–64.
- de la Torre, J. R., Goebel, B. M., Friedmann, E. I., and Pace, N. R. (2003). Microbial diversity of cryptoendolithic communities from the McMurdo Dry Valleys, Antarctica. *Applied and Environmental Microbiology*, **69**, 3858–3867.
- DeSantis, T. Z., Hugenholtz, P., Larsen, N., et al. (2006). Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Applied and Environmental Microbiology*, **72**, 5069–5072.

- Dore, J. E. and Priscu, J. C. (2001). Phytoplankton phosphorus deficiency and alkaline phosphatase activity in the McMurdo Dry Valley lakes, Antarctica. *Limnology and Oceanography*, **46**, 1331–1346.
- Doran, P. T., Wharton, R. A., and Lyons, W. B. (1994). Paleolimnology of the McMurdo Dry Valleys, Antarctica. *Journal of Paleolimnology*, **10**, 85–114.
- Doran, P. T., Priscu, J. C., Lyons, W. B., et al. (2002). Antarctic climate cooling and terrestrial ecosystem response. *Nature*, **415**, 517–520.
- Doran, P. T., Fritsen, C. H., McKay, C. P., Priscu, J. C., and Adams, E. E. (2003). Formation and character of an ancient 19-m ice cover and underlying trapped brine in an “ice-sealed” east Antarctic lake. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 26–31.
- Dunbar, J., Takala, S., Barns, S. M., Davis, J. A., and Kuske, C. R. (1999). Levels of bacterial community diversity in four arid soils compared by cultivation and 16S rRNA gene cloning. *Applied and Environmental Microbiology*, **65**, 1662–1669.
- Esposito, R. M. M., Horn, S. L., McKnight, D. M., et al. (2006). Antarctic climate cooling and response of diatoms in glacial meltwater streams. *Geophysical Research Letters*, **33**, 1–4.
- Fell, J. W., Scorzetti, G., Connell, L., and Craig, S. (2006). Biodiversity of micro-eukaryotes in Antarctic Dry Valley soils with <5% soil moisture. *Soil Biology and Biochemistry*, **38**, 3107–3119.
- Fierer, N. and Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 626–631.
- Foreman, C. M., Sattler, B., Mikucki, J. A., Porazinska, D. L., and Priscu, J. C. (2007). Metabolic activity and diversity of cryoconites in the Taylor Valley, Antarctica. *Journal of Geophysical Research*, **112**, 1–11.
- Fountain, A., Tranter, M., Nylen, T., Lewis, K., and Mueller, D. (2004). Evolution of cryoconite holes and their contribution to meltwater runoff from glaciers in the McMurdo Dry Valleys, Antarctica. *Journal of Glaciology*, **50**, 35–45.
- Franzmann, P. D., Liu, Y., Balkwill, D. L., et al. (1997). *Methanogenium frigidum* sp. nov., a psychrophilic, H<sub>2</sub>-using methanogen from Ace Lake, Antarctica. *International Journal of Systematics and Bacteriology*, **47**, 1068–1072.
- Friedmann, E. I. (1993). *Antarctic Microbiology*. New York: Wiley-Liss.
- Friedmann, E. I., Hua, M., and Ocampo-Friedmann, R. (1988). Cryptoendolithic lichen and cyanobacterial communities of the Ross Desert, Antarctica. *Polarforschung*, **58**, 251–259.
- Fritsen, C. H. and Priscu, J. C. (1998). Cyanobacterial assemblages in permanent ice covers on Antarctic lakes: distribution, growth rate, and temperature response of photosynthesis. *Journal of Phycology*, **34**, 587–597.
- Fritsen, C. H., Adams, E. E., McKay, C. P., and Priscu, J. C. (1998). Permanent ice covers of the McMurdo Dry Valleys lakes, Antarctica: liquid water contents. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Priscu. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 269–280.
- Fritsen, C. H., Grue, A. M., and Priscu, J. C. (2000). Distribution of organic carbon and nitrogen in surface soils in the McMurdo Dry Valleys, Antarctica. *Polar Biology*, **23**, 121–128.
- Gause, G. F. (1934). *The Struggle for Existence*. Baltimore, MD: Williams and Wilkins.
- Gilichinsky, D. A. (2007). Microbial populations in Antarctic permafrost: biodiversity, state age, and implication for astrobiology. *Astrobiology*, **7**, 275–311.

- Glatz, R. E., Lepp, P. W., Ward, B. B., and Francis, C. A. (2006). Planktonic microbial community composition across steep physical/chemical gradients in permanently ice-covered Lake Bonney, Antarctica. *Geobiology*, **4**, 53–67.
- Glausiusz, J. (2007). Extreme culture. *Nature*, **447**, 905–906.
- Goldman, C. R. (1964). Primary productivity studies in Antarctic lakes. In *Biologie Antarctique*. Proceedings of 1st SCAR symposium, ed. R. Carrick, M. Holgate, and J. Prevost. Paris: Hermann, pp. 291–299.
- Goldman, C. R., Mason, D. T., and Hobbie, J. E. (1967). Two Antarctic desert lakes. *Limnology and Oceanography*, **12**, 295–310.
- Gordon, D. A., Priscu, J., and Giovannoni, S. (2000). Origin and phylogeny of microbes living in permanent Antarctic lake ice. *Microbial Ecology*, **39**, 197–202.
- Hall, J., Mitchell, K., Jackson-Weaver, O., et al. (2008). Molecular characterization of the diversity and distribution of a thermal spring microbial community using rRNA and functional genes. *Applied and Environmental Microbiology*, **74**, 4910–4922.
- Hardin, G. (1960). The competitive exclusion principle. *Science*, **131**, 1292–1297.
- Hogg, I. D., Craig Cary, S., Convey, P., et al. (2006). Biotic interactions in Antarctic terrestrial ecosystems: are they a factor? *Soil Biology and Biochemistry*, **38**, 3035–3040.
- Hopkins, D. W., Sparrow, A. D., Novis, P. M., et al. (2006). Controls on the distribution of productivity and organic resources in Antarctic Dry Valley soils. *Proceedings of the Royal Society of London, Biological Sciences*, **273**, 2687–2695.
- Horner-Devine, M. C., Carney, K. M., and Bohannan, B. J. M. (2003). An ecological perspective on bacterial biodiversity. *Proceedings of the Royal Society of London, Series B*, **271**, 113–122.
- Horner-Devine, M. C., Silver, J. M., Leibold, M. A., et al. (2007). A comparison of taxon co-occurrence for macro- and microorganisms. *Ecology*, **88**, 1345–1353.
- Horowitz, N. H., Cameron, R. E., and Hubbard, J. S. (1972). Microbiology of the Dry Valleys of Antarctica. *Science*, **176**, 242–245.
- Howard-Williams, C., Schwarz, A. M., Hawes, I., and Priscu, J. C. (1998). Optical properties of the McMurdo Dry Valley lakes, Antarctica. *Antarctic Research Series*, **72**, 189–203.
- Hughes, J. B., Hellmann, J. J., Ricketts, T. H., and Bohannan, B. J. (2001). Counting the uncountable: statistical approaches to estimating microbial diversity. *Applied and Environmental Microbiology*, **67**, 4399–4406.
- Huston, M. (1979). A general hypothesis of species diversity. *American Naturalist*, **113**, 81.
- Hutchinson, G. E. (1961). The paradox of the plankton. *American Naturalist*, **95**, 137–145.
- Jones, J. and Simon, B. (1985). Interaction of acetogens and methanogens in anaerobic freshwater sediments. *Applied and Environmental Microbiology*, **49**, 944–948.
- Jung, D. O., Achenbach, L. A., Karr, E. A., Takaichi, S., and Madigan, M. T. (2004). A gas vesiculate planktonic strain of the purple non-sulfur bacterium *Rhodospirillum rubrum* isolated from Lake Fryxell, Dry Valleys, Antarctica. *Archives of Microbiology*, **182**, 236–243.
- Karr, E. A., Sattley, W. M., Jung, D. O., Madigan, M. T., and Achenbach, L. A. (2003). Remarkable diversity of phototrophic purple bacteria in a permanently frozen Antarctic lake. *Applied and Environmental Microbiology*, **69**, 4910–4914.
- Karr, E. A., Sattley, W. M., Rice, M. R., et al. (2005). Diversity and distribution of sulfate-reducing bacteria in permanently frozen Lake Fryxell, McMurdo Dry Valleys, Antarctica. *Applied and Environmental Microbiology*, **71**, 6353–6359.

- Karr, E. A., Ng, J. M., Belchik, S. M., et al. (2006). Biodiversity of methanogenic and other archaea in the permanently frozen Lake Fryxell, Antarctica. *Applied and Environmental Microbiology*, **72**, 1663–1666.
- Kepner, Jr., R. L., Wharton, Jr., R. A., and Suttle, C. A. (1998). Viruses in Antarctic lakes. *Limnology and Oceanography*, **43**, 1754–1761.
- Kepner, R. L., Wharton, Jr., R. A., and Coats, D. W. (1999). Ciliated protozoa of two Antarctic lakes: analysis by quantitative protargol staining and examination of artificial substrates. *Polar Biology*, **21**, 285–294.
- Koob, D. D. and Leister, G. L. (1972). Primary productivity and associated physical chemical and biological characteristics of Lake Bonney: a perennially ice-covered lake in Antarctica. *Antarctic Research Series*, **20**, 51–68.
- Krembs, C., Juhl, A. R., Long, R. A., and Azam, F. (1998). Nanoscale patchiness of bacteria in lake water studied with the spatial information preservation method. *Limnology and Oceanography*, **43**, 307–314.
- Lancaster, N. (2002). Flux of eolian sediment in the McMurdo Dry Valleys, Antarctica: a preliminary assessment. *Arctic Antarctic and Alpine Research*, **34**, 318–323.
- Laybourn-Parry, J. (1997). The microbial loop in Antarctic lakes. In *Ecosystems Processes in Antarctic Ice-Free Landscapes*, ed. W. B. Lyons, C. Howard-Williams, and I. Hawes. Rotterdam, Netherlands: A. A. Balkema, pp. 231–240.
- Lee, P. A., Mikucki, J. A., Foreman, C. M., et al. (2004). Thermodynamic constraints on microbially mediated processes in lakes of the McMurdo Dry Valleys, Antarctica. *Geomicrobiology Journal*, **21**, 221–237.
- Levins, R. (1968). *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.
- Lisle, J. T. and Priscu, J. C. (2004). The occurrence of lysogenic bacteria and microbial aggregates in the lakes of the McMurdo Dry Valleys, Antarctica. *Microbial Ecology*, **47**, 427–439.
- Lizotte, M. P. and Priscu, J. C. (1992). Spectral irradiance and bio-optical properties in perennially ice-covered lakes of the Dry Valleys (McMurdo Sound, Antarctica). *Antarctic Research Series*, **57**, 1–14.
- Lizotte, M. P., Sharp, T. R., and Priscu, J. C. (1996). Phytoplankton dynamics in the stratified water column of Lake Bonney, Antarctica. I. Biomass and productivity during the winter-spring transition. *Polar Biology*, **16**, 155–162.
- Lozupone, C. and Knight, R. (2005). UniFrac: a new phylogenetic method for comparing microbial communities. *Applied and Environmental Microbiology*, **71**, 8228–8235.
- Lozupone, C. A. and Knight, R. (2007). Global patterns in bacterial diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 11436.
- Lyons, W. B., Welch, K. A., Neumann, K., et al. (1998). Geochemical linkages among glaciers, streams and lakes within the Taylor Valley, Antarctica. *Antarctic Research Series*, **72**, 77–92.
- Lyons, W. B., Tyler, S. W., Wharton, R. A., McKnight, D. M., and Vaughn, B. H. (2004). A Late Holocene desiccation of Lake Hoare and Lake Fryxell, McMurdo Dry Valleys, Antarctica. *Antarctic Science*, **10**, 247–256.
- Madigan, M. T., Jung, D. O., Woese, C. R., and Achenbach, L. A. (2000). *Rhodoferrax antarcticus* sp. nov., a moderately psychrophilic purple nonsulfur bacterium isolated from an Antarctic microbial mat. *Archives of Microbiology*, **173**, 269–277.
- Magurran, A. E. (2004). *Measuring Biological Diversity*. Oxford, UK: Blackwell.



- Matsubaya, O., Sakai, H., Torii, T., Burton, H., and Kerry, K. (1979). Antarctic saline lakes: stable isotopic ratios, chemical compositions and evolution. *Geochimica et Cosmochimica Acta*, **43**, 7–25.
- May, R. M. (1974). On the theory of niche overlap. *Theoretical Population Biology*, **5**, 297–332.
- May, R. M. (1975). Patterns of species abundance and diversity. *Ecology and Evolution of Communities*, **1**, 81–120.
- McKay, C. P., Andersen, D. T., Wayne, H., et al. (2005). Polar lakes, streams, and springs as analogs for the hydrological cycle on Mars. In *Water on Mars and Life*, ed. T. Tokano. Heidelberg, Germany: Springer, pp. 219–233.
- McKnight, D. M., Alger, A., Tate, C. M., Shupe, G., and Spaulding, S. (1998). Longitudinal patterns in algal abundance and species distribution in meltwater streams in Taylor Valley, Southern Victoria Land, Antarctica. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Prisco. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 109–127.
- McKnight, D. M., Niyogi, D. K., Alger, A. S., et al. (1999). Dry valley streams in Antarctica: ecosystems waiting for water. *BioScience*, **49**, 985–995.
- McKnight, D. M., Tate, C. M., Andrews, E. D., et al. (2007). Reactivation of a cryptobiotic stream ecosystem in the McMurdo Dry Valleys, Antarctica: a long-term geomorphological experiment. *Geomorphology*, **89**, 186–204.
- Mikell, Jr., A. T., Parker, B. C., and Gregory, E. M. (1986). Factors affecting high-oxygen survival of heterotrophic microorganisms from an Antarctic lake. *Applied and Environmental Microbiology*, **52**, 1236–1241.
- Mikucki, J. A. (2005). Microbial ecology of an Antarctic subglacial environment. Ph.D. thesis, Montana State University, Bozeman, MT.
- Mikucki, J. A. and Prisco, J. C. (2007). Bacterial diversity associated with Blood Falls, a subglacial outflow from the Taylor Glacier, Antarctica. *Applied and Environmental Microbiology*, **73**, 4029–4039.
- Mosier, A. C., Murray, A. E., and Fritsen, C. H. (2007). Microbiota within the perennial ice cover of Lake Vida, Antarctica. *FEMS Microbiology Ecology*, **59**, 274–288.
- Nemergut, D. R., Costello, E. K., Meyer, A. F., et al. (2005). Structure and function of alpine and arctic soil microbial communities. *Research in Microbiology*, **156**, 775–784.
- Niederberger, T. D., McDonald, I. R., Hacker, A. L., et al. (2008). Microbial community composition in soils of northern Victoria Land, Antarctica. *Environmental Microbiology*, **10**, 1713–1724.
- Nkem, J. N., Wall, D. H., Virginia, R. A., et al. (2006). Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. *Polar Biology*, **29**, 346–352.
- Paerl, H. W. and Prisco, J. C. (1998). Microbial phototrophic, heterotrophic, and diazotrophic activities associated with aggregates in the permanent ice cover of Lake Bonney, Antarctica. *Microbial Ecology*, **36**, 221–230.
- Paine, R. T. (1966). Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.
- Parker, B. C., Hoehn, R. C., Paterson, R. A., et al. (1977). Changes in dissolved organic matter, photosynthetic production and microbial community composition in Lake Bonney, southern Victoria Land, Antarctica. In *Adaptations within Antarctic Ecosystems*, ed. G. Llano. Washington, D.C.: Smithsonian Institution, pp. 859–872.

- Parker, B. C., Simmons, G. M., Wharton, R. A., Seaburg, K. G., and Love, F. G. (1982). Removal of organic and inorganic matter from Antarctic lakes by aerial escape of bluegreen algal mats. *Journal of Phycology*, **18**, 72–78.
- Poff, N. L. and Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1817.
- Porazinska, D. L., Fountain, A. G., Nysten, T. H., et al. (2004). The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley glaciers, Antarctica. *Arctic Antarctic and Alpine Research*, **36**, 84–91.
- Priscu, J. C. (1995). Phytoplankton nutrient deficiency in lakes of the McMurdo Dry Valleys, Antarctica. *Freshwater Biology*, **34**, 215–227.
- Priscu, J. C., Downes, M. T., and McKay, C. P. (1996). Extreme supersaturation of nitrous oxide in a poorly ventilated Antarctic lake. *Limnology and Oceanography*, **41**, 1544–1551.
- Priscu, J. C., Fritsen, C. H., Adams, E. E., et al. (1998). Perennial Antarctic lake ice: an oasis for life in a polar desert. *Science*, **280**, 2095–2098.
- Priscu, J. C., Wolf, C. F., Takacs, C. D., et al. (1999). Carbon transformations in a perennially ice-covered Antarctic lake. *BioScience*, **49**, 997–1008.
- Priscu, J. C., Vincent, W. F., and Howard-Williams, C. (2002). Inorganic nitrogen uptake and regeneration in perennially ice-covered Lakes Fryxell and Vanda, Antarctica. *Journal of Plankton Research*, **11**, 335–351.
- Priscu, J. C., Christner, B. C., Dore, J. E., et al. (2008). Supersaturated N<sub>2</sub>O in a perennially ice-covered lake: molecular and stable isotopic evidence for a biogeochemical relict. *Limnology and Oceanography*, **53**(6), 2439–2450.
- Roberts, E. C. and Laybourn-Parry, J. (1999). Mixotrophic cryptophytes and their predators in the Dry Valley lakes of Antarctica. *Freshwater Biology*, **41**, 737–746.
- Roberts, E. C., Laybourn-Parry, J., McKnight, D. M., and Novarino, G. (2000). Stratification and dynamics of microbial loop communities in Lake Fryxell, Antarctica. *Freshwater Biology*, **44**, 649–661.
- Roberts, E. C., Priscu, J. C., Wolf, C., Lyons, W. B., and Laybourn-Parry, J. (2004). The distribution of microplankton in the McMurdo Dry Valley lakes, Antarctica: response to ecosystem legacy or present-day climatic controls? *Polar Biology*, **27**, 238–249.
- Roth, R. R. (1976). Spatial heterogeneity and bird species diversity. *Ecology*, **57**, 773–782.
- Runkel, R. L., McKnight, D. M., and Andrews, E. D. (1998). Analysis of transient storage subject to unsteady flow: diel flow variation in an Antarctic stream. *Journal of the North American Benthological Society*, **17**, 143–154.
- Sattley, W. M. and Madigan, M. T. (2006). Isolation, characterization, and ecology of cold-active, chemolithotrophic, sulfur-oxidizing bacteria from perennially ice-covered Lake Fryxell, Antarctica. *Applied and Environmental Microbiology*, **72**, 5562–5568.
- Sattley, W. M. and Madigan, M. T. (2007). Cold-active acetogenic bacteria from surficial sediments of perennially ice-covered Lake Fryxell, Antarctica. *FEMS Microbiology Letters*, **272**, 48–54.
- Sävström, C., Lisle, J., Anesio, A. M., Priscu, J. C., and Laybourn-Parry, J. (2008). Bacteriophage in polar inland waters. *Extremophiles*, **12**, 167–175.
- Schoener, T. W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology*, **6**, 265–307.
- Schwarz, A. M. J., Green, T. G. A., and Seppelt, R. D. (1992). Terrestrial vegetation at Canada Glacier, southern Victoria Land, Antarctica. *Polar Biology*, **12**, 397–404.

- Scott, R. F. (1905). *The Voyage of the "Discovery"*. New York: C. Scribner's Sons.
- Shivaji, S., Reddy, G. S. N., Suresh, K., et al. (2005). *Psychrobacter vallis* sp. nov. and *Psychrobacter aquaticus* sp. nov., from Antarctica. *International Journal of Systematic and Evolutionary Microbiology*, **55**, 757–762.
- Skotnicki, M. L., Ninham, J. A., and Selkirk, P. M. (2000). Genetic diversity, mutagenesis and dispersal of Antarctic mosses: a review of progress with molecular studies. *Antarctic Science*, **12**, 363–373.
- Smith, J. J., Tow, L. A., Stafford, W., Cary, C., and Cowan, D. A. (2006). Bacterial diversity in three different Antarctic cold desert mineral soils. *Microbial Ecology*, **51**, 413–421.
- Sommer, U. (1985). Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. *Limnology and Oceanography*, **30**, 335–346.
- Spigel, R. H. and Priscu, J. C. (1998). Physical limnology of the McMurdo Dry Valley lakes. In *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*, ed. J. C. Priscu. Antarctic Research Series 72. Washington, D.C.: American Geophysical Union, pp. 153–187.
- Stackebrandt, E., Brambilla, E., Cousin, S., Dirks, W., and Pukall, R. (2004). Culture-independent analysis of bacterial species from an anaerobic mat from Lake Fryxell, Antarctica: prokaryotic diversity revisited. *Cellular and Molecular Biology*, **50**, 517–524.
- Stingl, U., Cho, J. C., Foo, W., et al. (2008). Dilution-to-extinction culturing of psychrotolerant planktonic bacteria from permanently ice-covered lakes in the McMurdo Dry Valleys, Antarctica. *Microbial Ecology*, **55**, 395–405.
- Takacs, C. D. and Priscu, J. C. (1998). Bacterioplankton dynamics in the McMurdo Dry Valley lakes, Antarctica: production and biomass loss over four seasons. *Microbial Ecology*, **36**, 239–250.
- Takacs, C. D., Priscu, J. C., and McKnight, D. M. (2001). Bacterial dissolved organic carbon demand in McMurdo Dry Valley lakes, Antarctica. *Limnology and Oceanography*, **46**, 1189–1194.
- Takacs-Vesbach, C., Mitchell, K., Jackson-Weaver, O., and Reysenbach, A. L. (2008). Volcanic calderas delineate biogeographic provinces among Yellowstone thermophiles. *Environmental Microbiology*, **10**, 1681–1689.
- Taton, A., Grubisic, S., Brambilla, E., De Wit, R., and Wilmotte, A. (2003). Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo Dry Valleys, Antarctica): a morphological and molecular approach. *Applied and Environmental Microbiology*, **69**, 5157–5169.
- Thompson, J. R., Pacocha, S., Pharino, C., et al. (2005). Genotypic diversity within a natural coastal bacterioplankton population. *Science*, **307**, 1311–1313.
- Tilman, D., Kilham, S. S., and Kilham, P. (1982). Phytoplankton community ecology: the role of limiting nutrients. *Annual Reviews in Ecology and Systematics*, **13**, 349–372.
- Tindall, B. J., Brambilla, E., Steffen, M., et al. (2000). Cultivable microbial biodiversity: gnawing at the Gordian knot. *Environmental Microbiology*, **2**, 310–318.
- Torsvik, V., Ovreas, L., and Thingstad, T. F. (2002). Prokaryotic diversity: magnitude, dynamics, and controlling factors. *Science*, **296**, 1064–1066.
- Townsend, C. R., Scarsbrook, M. R., and Doledec, S. (1997). The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography*, **42**, 938–949.

- Treonis, A. M., Wall, D. H., and Virginia, R. A. (1999). Invertebrate biodiversity in Antarctic dry valley soils and sediments. *Ecosystems*, **2**, 482–492.
- Urbach, E., Vergin, K. L., Young, L., et al. (2001). Unusual bacterioplankton community structure in ultra-oligotrophic Crater Lake. *Limnology and Oceanography*, **46**, 557–572.
- Urbach, E., Vergin, K. L., Larson, G. L., and Giovannoni, S. J. (2007). Bacterioplankton communities of Crater Lake, Oregon: dynamic changes with euphotic zone food web structure and stable deep water populations. *Hydrobiologia*, **574**, 161–177.
- Van Trappen, S., Mergaert, J., Van Eygen, S., et al. (2002). Diversity of 746 heterotrophic bacteria isolated from microbial mats from ten Antarctic lakes. *Systematic and Applied Microbiology*, **25**, 603–610.
- Van Trappen, S., Vandecandelaere, I., Mergaert, J., and Swings, J. (2004). *Algoriphagus antarcticus* sp. nov., a novel psychrophile from microbial mats in Antarctic lakes. *International Journal of Systematic and Evolutionary Microbiology*, **54**, 1969–1973.
- Vincent, W. F. (1981). Production strategies in Antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. *Ecology*, **62**, 1215–1224.
- Vincent, W. F. (1988). *Microbial Ecosystems of Antarctica*. New York: Cambridge University Press.
- Vincent, W. F. and Howard-Williams, C. (1986). Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biology*, **16**, 219–233.
- Vincent, W. F. and Howard-Williams, C. (1989). Microbial communities in Southern Victoria Land streams (Antarctica). II. The effects of low temperature. *Hydrobiologia*, **172**, 39–49.
- Vincent, W. F. and James, M. R. (1996). Biodiversity in extreme aquatic environments: lakes, ponds and streams of the Ross Sea Sector, Antarctica. *Biodiversity and Conservation*, **5**, 1451–1471.
- Vincent, W. F., Rae, R., Laurion, I., Howard-Williams, C., and Priscu, J. C. (1998). Transparency of Antarctic ice-covered lakes to solar UV radiation. *Limnology and Oceanography*, **43**, 618–624.
- Virginia, R. A. and Wall, D. H. (1999). How soils structure communities in the Antarctic Dry Valleys. *BioScience*, **49**, 973–983.
- Vishniac, H. S. (1993). The microbiology of Antarctic soils. In *Antarctic Microbiology*, ed. E. I. Friedmann. New York: Wiley-Liss, pp. 297–341.
- Voytek, M. A. and Ward, B. B. (1995). Detection of ammonium-oxidizing bacteria of the beta-subclass of the class Proteobacteria in aquatic samples with the PCR. *Applied and Environmental Microbiology*, **61**, 1444–1450.
- Voytek, M. A., Priscu, J. C., and Ward, B. B. (1999). The distribution and relative abundance of ammonia-oxidizing bacteria in lakes of the McMurdo Dry Valley, Antarctica. *Hydrobiologia*, **401**, 113–130.
- Ward, B. B. and Priscu, J. C. (1997). Detection and characterization of denitrifying bacteria from a permanently ice-covered Antarctic lake. *Hydrobiologia*, **347**, 57–68.
- Ward, B. B., Granger, J., Maldonado, M. T., et al. (2005). Denitrification in the hypolimnion of permanently ice-covered Lake Bonney, Antarctica. *Aquatic Microbial Ecology*, **38**, 295–307.
- Ward, D. M. (1998). A natural species concept for prokaryotes. *Current Opinion in Microbiology*, **1**, 271–277.

- Ward, D. M., Cohan, F. M., Bhaya, D., et al. (2008). Genomics, environmental genomics and the issue of microbial species. *Heredity*, **100**, 207–219.
- Wharton, Jr., R. A., McKay, C. P., Simmons, Jr., G. M., and Parker, B. C. (1985). Cryoconite holes on glaciers. *BioScience*, **35**, 499–503.
- Wynn-Williams, D. D. and Edwards, H. G. M. (2000). Antarctic ecosystems as models for extraterrestrial surface habitats. *Planetary and Space Science*, **48**, 1065–1075.
- Young, I. M. and Ritz, K. (2000). Tillage, habitat space and function of soil microbes. *Soil and Tillage Research*, **53**, 201–213.
- Zeglin, L. (2008). Microbial diversity and function at aquatic-terrestrial interfaces in desert ecosystems. Ph.D. thesis, University of New Mexico, Albuquerque, NM.
- Zeglin, L., Sinsabaugh, R., Barrett, J. E., Gooseff, M., and Takacs-Vesbach, C. (2009). Landscape distribution of microbial activity in the McMurdo Dry Valleys: linked biotic processes, hydrology and geochemistry in a cold desert ecosystem. *Ecosystems*, **12**(4), 562–573.
- Zhou, J., Xia, B., Treves, D. S., et al. (2002). Spatial and resource factors influencing high microbial diversity in soil. *Applied and Environmental Microbiology*, **68**, 326–334.