Landscape history and contemporary environmental drivers of microbial community structure and function

Adam Edward Altrichter

Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Master of Science
In
Biological Sciences

John E. Barrett (chair)
Jackson R. Webster
Michael N. Gooseff
Randolph H. Wynne

April 10, 2012
Blacksburg, Virginia

Keywords: McMurdo Dry Valleys, microbial biogeography, T-RFLP, community similarity, extracellular enzyme activity, soil geochemistry

Landscape history and contemporary environmental drivers of microbial community structure and function

Adam Edward Altrichter

ABSTRACT

Recent work in microbial ecology has focused on elucidating controls over biogeographic patterns and connecting microbial community composition to ecosystem function. My objective was to investigate the relative influences of landscape legacies and contemporary environmental factors on the distribution of soil microbial communities and their contribution to ecosystem processes across a glacial till sequence in Taylor Valley, Antarctica. Within each till unit, I sampled from dry areas and areas with visible evidence of recent surface water movement generated by seasonal melting of ephemeral snow packs and hillslope ground ice. Using T-RFLP 16S rRNA gene profiles of microbial communities, I analyzed the contribution of till and environmental factors to community similarity, and assessed the functional potential of the microbial community using extracellular enzyme activity assays. Microbial communities were influenced by geochemical differences among both tills and local environments, but especially organized by variables associated with water availability as the first axis of an NMDS ordination was strongly related to shifts in soil moisture content. CCA revealed that tills explained only 3.4% of the variability in community similarity among sites, while geochemical variables explained 18.5%. Extracellular enzyme activity was correlated with relevant geochemical variables reflecting the influence of nutrient limitation on microbial activity. In addition, enzyme activity was related to changes in community similarity, particularly in wet environments with a partial Mantel correlation of 0.32. These results demonstrate how landscape history and environmental conditions can shape the functional potential of a microbial community mediated through shifts in microbial community composition.

ACKNOWLEDGEMENTS

I have been exceptionally lucky to be part of an incredible group of students, faculty, staff, and friends here at Virginia Tech. I have many people to thank for helping me throughout my career here and I couldn't have done it without their support, assistance, and training.

First and foremost, I have to thank my adviser, Jeb Barrett. Jeb took me on as a student knowing I came to work in streams and turned me onto the world of soils. He has provided me with training in the lab and field that will serve me well throughout my career. He took a gamble on me and allowed me to get involved in molecular analysis of microbial communities even though I hadn't ever taken a microbiology course. Ultimately, I have grown and learned more from struggling than I ever could have if he had let me take an easy way out. Not to mention, he provided me with the incredible opportunity to broaden my horizons to the Antarctic. Years from now, everything I learned in the classroom or lab will probably pale in comparison to everything I gained from the months I spent travelling and working in the field with him.

In those travels I was accompanied by a group of fellow researchers who made the experience enriching from both scientific and social perspectives. Kevin Geyer has been a great friend, travel buddy, field associate, and collaborator back in Blacksburg. He provided feedback throughout this project and played a major role in its success. In addition, a big thanks goes out to Dave Van Horn, Jeff Eveland, Mike Gooseff, and Tina Takacs-Vesbach for making great field associates on B023. Furthermore, I have to thank Dave and Tina for all of the assistance they provided to Kevin and I while we were troubleshooting all of our molecular and enzyme activity methods—the countless emails and Skype conversations have made all the difference.

Back at Virginia Tech, the Stream Team/Ecosystem Research Group has been another vital component of my education and training. I have been challenged by my peers in this group and have learned so much from our weekly meetings and daily interaction in the office. I won't miss not having windows, but I will miss having the great friends from this group around all the time. In addition, the Barrett lab undergraduates have all been great workers and helped me to accomplish everything along the way.

Thank you to several people within the Department of Biological Sciences at Virginia Tech: Ann Stevens' lab for allowing me access to and training on their plate reader, Khidir Hilu's lab for space in their -80° C freezer, and Lisa Belden's lab for access to the gel doc, emergency pipet tips, and help along the way. And equally important, thank you to the administrative staff for the department who have helped me ship and receive packages from all over the world, fill out complicated accounting forms, and ultimately graduate successfully.

And finally, have been so fortunate to have my family only a few hours' drive away in North Carolina. Their support has always led me to work harder and to try to produce the best work I possibly can. I wouldn't be where I am today without them.

Thank you all.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ABBREVIATIONS

ADONIS: analysis of variance using distance matrices

AG: α-glucosidase

AP: alkaline phosphatase

BG: β-glucosidase

CCA: canonical correspondence analysis

EC: electrical conductivity

LAP: leucyl aminopeptidase

NMDS: non-metric multi-dimensional scaling

OTU: operational taxonomic unit

SOC: soil organic carbon

TN: total nitrogen

TIN: total inorganic nitrogen

T-RFLP: terminal restriction fragment length polymorphism

INTRODUCTION

Biologists have been studying the biogeography of plant and animal species since Von Humboldt in the 19th century (Billings 1985), but until recent developments in molecular techniques, the biogeography of microorganisms has been limited to culture-based studies, which were unable to isolate and enumerate the majority of microbial diversity in natural environments (Tiedje et al. 1999, Martiny et al. 2006). In fact, early descriptions of microbial communities rejected the notion that microbial taxa exhibited biogeographic patterns and that instead local environmental conditions determined which organisms among a common species pool of universally dispersed taxa could survive and contribute to community composition in a given environment (i.e. Baas Becking, 1934). After a decade of work using molecular approaches to evaluate the Baas Becking hypothesis in a variety of environments and across a range of spatial scales, many studies have clearly shown that microorganisms, especially bacterial communities, do exhibit biogeographic patterns. For example, studies describing species-area relationships and distance-decay relationships for community similarity (Horner-Devine et al. 2004, Green and Bohannan 2006) demonstrate that microbial communities exhibit non-random biogeographic patterns. Studies from a variety of ecosystems support the assertion that microbial communities exhibit patterns of spatial distribution that are correlated with environmental gradients such as salinity (Casamayor et al. 2002, Crump et al. 2004), pH (Fierer and Jackson 2006), water column depth (Ovreas et al. 1997), latitude (Staddon and Trevors 1998), and land use history (Buckley and Schmidt 2003).

Current research efforts in microbial ecology are now focused on elucidating the physical, biological, or geochemical controls underlying these observed spatial patterns in microbial communities, and the potential influence of microbial community composition on ecosystem functioning. Biogeographic and more recent metacommunity approaches in ecology have distinguished between historic and contemporary drivers of community assembly and composition. For example, Baas Becking's hypothesis explicitly rules out the role that dispersal or historic barriers and conditions may contribute to contemporary community dynamics for microorganisms, focusing instead on the role of contemporary environmental conditions: "everything is everywhere, but the environment selects" (Baas Becking 1934). Alternatively, historical conditions separating species and/or populations or imparting lasting legacies on

contemporary environments also potentially influence community composition and diversity (Martiny et al. 2006). Based upon these competing models describing microbial biogeography, Martiny et al. (2006) posited four alternative hypotheses explaining the spatial distribution of microbial communities: 1) microbial taxa have global dispersal capabilities and exhibit random distribution; 2) microorganisms have ubiquitous distribution, but composition of microbial communities is driven by contemporary environmental conditions ("Baas Becking hypothesis", Baas Becking 1934); 3) historical legacies control the distribution of microorganisms; or 4) environmental conditions and legacies both work to influence microbial spatial variation (Fig. 1 a-d, respectively). These hypotheses can be restated as two questions: do microbial communities exhibit spatial variation, and if so, is this variability controlled by contemporary conditions, historical events, or both?

Previous work has shown that historical conditions and contemporary environments can influence microbial biogeography (Whitaker et al. 2003, Green et al. 2004, Horner-Devine et al. 2004, Yannarell and Triplett 2005, Takacs-Vesbach et al. 2008). At spatial scales between 10-3000 km both historical and environmental influences are likely to be evident (Martiny et al. 2006). For example, Yannarell and Triplett (2005) found that differences in lake microbial communities were explained by regional separation (approximately 250 km) as well as environmental gradients of pH and Secchi depth. However this is not always the case, as Takacs-Vesbach et al. (2008) found that historical caldera formations in Yellowstone explained the biogeographic pattern in thermal spring microbial community composition to a greater extent than contemporary environmental factors such as geochemistry among sites approximately 100 km apart.

Understanding microbial community assembly has broader relevance beyond extending biogeographic theory to microorganisms. These studies also have the potential to address the influence of microbial diversity and composition on ecological processes, such as nutrient cycling, which is linked to microbial taxa that facilitate key biogeochemical processes (Schimel 1995, Bell et al. 2005, Reed and Martiny 2007, Strickland et al. 2009). For example, Strickland et al. (2009) reported that decomposition rates of leaf litter is strongly influenced by the source microbial community used to inoculate leaves at the start of the study. Thus, given the variation in microbial communities and the influence community structure can have on function,

understanding the factors influencing the biogeography of microbial communities can also elucidate the role they play in ecosystem function.

My objective was to investigate the relative influences of historic and contemporary environmental variation on the composition of soil microbial communities and their contribution to ecosystem processes by using a combination of molecular and soil enzyme activity approaches. I conducted this work in the McMurdo Dry Valleys of Antarctica where the harsh physical conditions, dynamic climate, and heterogeneous surface contribute to significant variation in soil properties, water availability, and biological communities over multiple scales (Gooseff et al. 2003, Barrett et al. 2004, Esposito et al. 2006, Poage et al. 2008, Levy et al. 2011). The McMurdo Dry Valleys have a well-documented glacial history (Denton et al. 1989, Hall and Denton 2000) that has an important influence on soil chemistry and soil biotic communities (Freckman and Virginia 1997, Burkins et al. 2000, Barrett et al. 2007, Bockheim 2008). Thus, glacial tills can be considered a historical legacy, while local scale patterns in soil hydrology (e.g. snow and subsurface ice melt) are a contemporary environmental influence on biological communities.

Site Description: Taylor Valley Glacial History and Contemporary Environments

The McMurdo Dry Valleys have been part of the Long Term Ecological Research network since 1993 and have been a site for ongoing ecological research for decades. The Dry Valleys are extreme polar deserts within the Transantarctic Mountain range and are one of the driest systems on earth, receiving less than 10 cm of precipitation annually (Fountain et al. 1999). Mean annual air temperatures range from -16° C to -21° C (Fountain et al. 1999, Doran 2002). The extremely low precipitation and freezing air temperatures create an environment where water is the most limiting factor to biological processes (Kennedy 1993). Biota are further exposed to frequent freeze-thaw cycles and elongated light-dark cycles, which limit biological activity and productivity (Fountain et al. 1999, Treonis et al. 1999).

The Dry Valleys are shaped largely by past climate conditions, which have regulated primary physical conditions such as glacial extent and lake levels (Priscu 1995, Lyons et al. 2000, Barrett et al. 2007). These legacies play a particularly important role dictating contemporary ecosystem properties such as organic matter content and quality and nutrient levels

and limitation (Priscu 1995, Fountain et al. 1999, Burkins et al. 2000, Barrett et al. 2007, 2009, 2010, Bate et al. 2008). Taylor Valley has been one of the most intensively studied valleys in the region and has a well-documented glacial history with distinct tills deposited during glacial advance and retreat (Denton et al. 1989, Hall and Denton 2000, Higgins et al. 2000a, Bockheim et al. 2008) (Fig. 2).

Taylor Valley is oriented in a SW-NE direction having been predominantly shaped by the Taylor Glacier, an outlet glacier from the East Antarctic Ice sheet, and attained its present day form prior to around 3.5 mya (Denton et al. 1971, Bockheim et al. 2008). The valley mouth opens into the McMurdo Sound of the Ross Sea. Several dry-bed alpine glaciers flow down from the Asgard Range to the north and the Kukri Hills to the south (Fountain et al. 1999, Bockheim et al. 2008).

Three forms of glacial activity have shaped Taylor Valley: advances of the Taylor Glacier, advances from the Ross Embayment, and advances of alpine glaciers down from higher elevations (Bockheim et al. 2008) (Fig. 2). The Taylor Glacier has advanced four times into Taylor Valley (down-valley) with the earliest three reaching the mouth of the valley (Denton et al. 1971, 1989, Higgins et al. 2000a, 2000b, Bockheim et al. 2008) (Fig. 2, Table 1). The Ross Sea ice sheet advanced westward (up-valley) around 23 kya and acted as an ice dam to form glacial Lake Washburn, inundating valley floor sediments possibly up to 222 m elevation during the last glacial maximum (Hall and Denton 2000). Around 12-12.5 kya the Ross Sea ice shelf receded from the mouth of Taylor Valley and lake levels declined (Hall and Denton 2000). The major tills of Taylor Valley were formed by the Taylor Glacier and Ross Sea ice shelf advances, although alpine glaciers appear to have advanced multiple times in the past largely in concert with Taylor Glacier (Higgins et al. 2000a) (Fig. 2). This arrangement of glaciers forms a complex history of glacial tills and landscape disturbances. Although these have been shown to influence soil chemistry and invertebrate communities (e.g. Courtright et al. 2001, Barrett et al. 2004, Poage et al. 2008), the influence of glacial tills on the distribution of microbial communities remains unknown.

In addition, glacial tills exhibit unique soil geochemistry and nutrient availability according to their geographic position and surface exposure age (Bockheim 1997, Michalski et al. 2005, Barrett et al. 2007) (Table 1). Dry Valley soils are classified as Gelisols with 70% classified as dry permafrost (anhyturbels) due to the lack of soil water to allow for cryoturbation,

17% containing salt-enriched horizons, and 36% having salt pans (Bockheim 1997, 2002). Soils are course-grained, greater than 90% sand, but often highly variable due to the local glacial and lacustrine history (Bockheim 1997, Burkins et al. 2000). Soil chemistry is strongly correlated with soil age as influenced by the deposition of aerosols and surface accumulation of soluble salts (Bockheim 1997). In coastal areas, Na^+ and Cl^- dominate soil salts, while further inland Na^+ and NO_3^- dominate, and intermediate soils are enriched in Na^+ and SO_4^- (Bockheim 1997, 2002). Soils are dominated by NO_3^- at higher elevations and nearer the polar plateau, where long term accumulation of dry deposition is possible under xerous and ultraxerous conditions (Bockheim 1997, 2002, Michalski et al. 2005). Phosphorus availability is determined by clast composition of the parent material (Blecker et al. 2006, Bate et al. 2008). Soils across a range of ages from 70 ky to 8 My do not appear to vary significantly in their total P concentration, indicating soil age might not be the most important variable determining P cycling and availability (Bate et al. 2008). Instead, the initial P content of the parent material is a likely primary driver in contemporary P pools. For example, soils in the Lake Fryxell basin have higher P availability due to the higher content of basalt in the Ross Sea tills even though the basin is also associated with greater weathering due a more benign microclimate and enhanced liquid water availability (Bate et al. 2008). Biotic variables such as chlorophyll *a* and invertebrate abundance also vary among glacial tills in Taylor Valley (Barrett et al. 2004). Sites within this valley have some of the lowest concentrations of soil organic matter in the world (Burkins et al. 2000). Biology is not only limited by physical factors such as temperature and precipitation but also through a paucity of organic matter and nutrient availability. In addition, the stoichiometric conditions of the soil environment are often outside the constraints for balanced growth (Barrett et al. 2007).

In the contemporary Dry Valley environment, the largest source of liquid water is derived from glacial melt streams from the alpine glaciers that flow down to the valley floor in three terminal lake basins; Fryxell, Hoare, and Bonney (from east to west). These streams only flow for 4-12 weeks during the austral summer when temperatures and radiation are high enough to melt the glacier surface (Fountain et al. 1999). However, streams and lakes supply only a small fraction of the expansive arid soil environments with water because of their limited spatial extent. Instead, seasonal snowfall and ground ice are the two main sources of water available to the arid soils. Recent studies have shown that although the loss of water due to sublimation may

rapidly decrease the size of snow patches, which accumulate in shallow depressions throughout the landscape, they do significantly influence the soil moisture , geochemistry, and metazoan communities (Gooseff et al. 2003). Flowpaths are visible down gradient from many snow packs, with the largest packs contributing significantly more to water flow (e.g. Lyons et al. 2005).

Meltwater flowpaths are characterized as ephemeral subsurface meltwater flowpaths originating from either ground ice or larger snow packs (Harris et al. 2007). These flowpaths are often visible as dark, wet streaks down gradient from large snow packs, but often moisture is only evident 5-10 cm below the surface (Levy et al. 2011). Meltwater flowpaths generally have higher total dissolved solids and ion concentrations compared to glacial melt streams (Lyons et al. 2005, Harris et al. 2007) and total solute mass delivered to lakes by flowpaths may equal or exceed stream inputs (Levy et al. 2011). Furthermore, some of these meltwater flowpaths demonstrate unique solute concentrations and ratios that point to unique origins and weathering processes occurring in subsurface soils (Lyons et al. 2005, Harris et al. 2007). Taylor Valley is underlain by permafrost, similar to the other McMurdo Dry Valley soils, where 42% contain dry permafrost within 1 meter of the active layer and ice-cemented permafrost is found in drifts near the coast and in alpine drifts in Taylor Valley (Bockheim 2002). Given its ubiquitous distribution, meltwater flowpaths derived from ground ice melt may be an important source of soil moisture. Because of these limitations to soil water and their unique geochemical characteristics, meltwater flowpaths might provide an environmental control on microbial community composition.

METHODS

Sampling Description

To characterize soil bacterial communities I collected samples from the top 10 centimeters of soil with ethanol sterilized scoops and gloves. Samples were split into two subsamples: bulk soil for geochemical analysis and a subsample for molecular analysis of the microbial community preserved with sucrose-lysis buffer (SLB; 20 mM EDTA, 400 mM NaCl, 0.75 M sucrose, 50 mM Tris-HCl, pH 9) (Mitchell and Takacs-Vesbach 2008). I sampled in triplicate from 24 sites in the 4 major tills of Taylor Valley: 6 sites in Ross, 8 sites in Taylor II, 4 sites in Taylor III, and 6 sites in Taylor IV. Half of the sites within each till were sampled from within visible flowpaths of seasonal meltwater from snow packs or ground ice and the other half were sampled from areas that were not visibly wetted and were likely to be continuously dry from year to year. Dry sites tended to be at the tops of small topographic rises where snow was unlikely to accumulate and were not down gradient from other sources of meltwater. Bulk soil samples were stored at -20° C and SLB preserved soils for microbial community analysis were stored at -80° C and shipped back to Virginia Tech for further analyses.

Geochemical Analyses

Each soil sample was analyzed for gravimetric water content and oven dry weight equivalence by mass loss after 24 hours at 105° C (Barrett et al. 2004). I measured soil pH and electrical conductivity (EC) by soil: deionized water dilutions of 1:2 and 1:5, respectively (Nkem et al. 2006a). I determined soil organic carbon (SOC) and total nitrogen (TN) on dried, ground, and acidified sub-samples on an Elantech NC Soil Analyzer (Barrett et al. 2009). Inorganic nitrogen fractions, NH_4-N and NO_3-N, were determined on a sub-sample extracted in 2.0 M KCl and analyzed on a Lachat QuickChem autoanalyzer (Barrett et al. 2002). Total inorganic nitrogen (TIN) was calculated as the sum of NH_4-N and NO_3-N concentrations. Bioavailable phosphorus was determined through extraction in 0.5 M $NaHCO_3$ (pH 8.5) shaken for 30 minutes on an orbital shaker, acidified, and run on a Lachat QuickChem autoanalyzer (Cross and Schlesinger 2001, Bate et al. 2008). Microbial biomass was analyzed on subsamples incubated for 5 days in a

chloroform atmosphere chamber, then the chloroform labile carbon was extracted in 0.5 M K_2SO_4 and measured on an OI Analytical TOC Analyzer (Cheng and Virginia 1993).

Microbial Community Analyses

I extracted soil DNA using a modification of the CTAB procedure (Mitchell and Takacs-Vesbach 2008). Briefly, 0.7 g of SLB-preserved soil was added to 2 volumes of 1% CTAB buffer (1% CTAB, 0.75 M NaCl, 50 mM Tris pH 8, 10 mM EDTA), Lysozyme (final concentration 1 µg mL^{-1}), and Proteinase K (final concentration 200 µg mL^{-1}) and incubated at 60 C for 30 minutes. 10% SDS was added (final concentration 4%) and incubated at 60 C for another 30 minutes. Samples were then bead beat with 0.75 g of 0.1 mm Zirconia/Silica beads for 30 seconds, extracted once with phenol/chloroform/isoamyl alcohol (25:24:1), extracted once with chloroform, then precipitated with 0.1 volumes of 3 M NaOAC and 2 volumes 95% ethanol overnight at -20 C, and finally washed again with 70% ethanol.

Microbial communities were assessed using the microbial community fingerprint method based upon terminal restriction fragment length polymorphism (T-RFLP). This method allowed us to compare microbial community structure and diversity across many samples efficiently and with high reproducibility (Liu et al. 1997, Osborn et al. 2000). Briefly, T-RFLP involves PCR amplification between two highly conserved primer-attaching regions of DNA, with variability between primer locations indicative of taxa identity. The amplified DNA is tagged with a fluorescent molecule on one end of the amplicon, subjected to restriction enzyme digestion, and then run through a capillary sequencer to obtain a peak height and number of peaks for each segment of fluoroprobe-attached DNA. I amplified16S rRNA genes using 8F with fluorescent molecule 6-FAM modification (5' 6FAM-AGA GTT TGA TCM TGG CTC AG 3') and 519R primers (5′ CCG CGG CKG CTG GCA C 3') (IDT Inc., Coralville, IA). Each PCR reaction contained 0.2 µM each primer, 200 µM each dNTP, 2.5 m M MgCl2, 1 unit Taq polymerase (Promega Corp., Fitchburg, WI), 1x Taq buffer, and 2 µL of 1:100 diluted template DNA. The low and highly variable microbial biomass of this system prevented standardization of DNA quantity across all PCR reactions, however upon analysis by NanoDrop spectrophotometer to determine quality (260:280 nm ratio) of extracted DNA, there was no significant influence of environments or tills ($p = 0.241$) and there was a non-significant regression ($p = 0.113$)

predicting T-RFLP richness from extracted DNA concentration. PCR reaction protocol began with 2 minutes hot start at 95° C, then 30 cycles each of 95° C for 30 seconds, 58° C for 30 seconds, and 72° C for 1 minute, followed by a final extension at 72° C for 10 min. I was unable to amplify 4 samples apparently due to high salinity levels, which prevented quality DNA extraction, therefore the sample set was reduced to 68 samples.

Restriction enzyme digestions were run with 200 ng of amplified DNA with HaeIII (New England BioLabs, Ipswich, MA) for 3 hours at 37° C followed by heat inactivation. Each sample was run with four replicates on an ABI 3130xl capillary sequencer. Samples were cleaned using GenScript QuickClean II PCR Extraction Kit after initial amplification and prior to running on capillary sequencer.

Extracellular Enzyme Activity Assays

Assays to determine potential soil enzyme activity were carried out on each sample with a method optimized for the low OM content of Antarctic soils as described by Zeglin et al. (2009). I assayed a total of 4 hydrolytic soil enzymes: 2 carbon acquiring enzymes, α-glucosidase (AG, EC 3.2.1.20; using 4-Methylumbelliferyl (MUB)-α-D-glucopyranoside, CAS 17833-43-1) and β-glucosidase (BG, EC 3.2.1.21; using 4-MUB-β-D-glucopyranoside, CAS 18997-57-4); one nitrogen acquiring enzyme, leucyl aminopeptidase (LAP, EC 3.4.11.1; using L-Leucine-7-amido-4-methylcoumarin hydrochloride, CAS 62480-44-8); and one phosphorus acquiring enzyme, alkaline phosphatase (AP, EC 3.1.3.1 ; using 4-MUB-phosphate, CAS 3368-04-5). Assays were completed with three replicate samples containing 0.5 g of soil, with 700 µL of substrate solution (200 µM) and 700 µL of 50 mM $NaHCO_3$ buffer (pH 8.2). Each sample for each enzyme was run with a negative control (0.5 g soil and 1400 µL of 50 mM $NaHCO_3$ buffer) and also a quenched standard (0.5 g soil, 700 µL of 50 mM $NaHCO_3$ buffer, and 700 µL of 10 µM standard) to correct for background fluorescence and sample-specific inhibition. AG, BG, and AP all used 4-MUB (CAS 90-33-5) standard, and LAP used 7-amino-4-methylcoumarin (CAS 26093-31-2) standard. I standardized all activity levels to nmol h^{-1} g^{-1} OM, assuming a correction of 1.9 from soil carbon to organic matter (OM) for surface soils (Broadbent 1953, Nelson and Sommers 1982). I compared relative nutrient limitation by calculating ratios of

BG:LAP, BG:AP, and LAP:AP enzyme activity to represent C:N, C:P, and N:P requirements of the microbes.

Statistics and Data Analysis

All geochemical and enzyme activity data were log-transformed (except for pH) to improve normality of the data and z-score standardized prior to statistical analysis (Legendre and Legendre 1998). Soil geochemistry and enzyme activity was compared among environments (wet and dry) and till category using a two-way ANOVA, and I compared means with a post-hoc Tukey's HSD in JMP 9.0 (SAS Institute Inc.). I used multiple linear regressions to predict enzyme activity from soil characteristics (water content, pH, EC, TOC, TN, NO_3-N, NH_4-N, and microbial biomass) using a forward selection method in JMP 9.0 (SAS Institute Inc.).

I used GeneMarker (SoftGenetics, LLC) software to obtain profiles generated by the capillary sequencer from each sample excluding those peaks below 25 fluorescence units (FU). Standardization of total profile FU was done among replicates and across all samples according to methods described by Dunbar et al. (2001) in order to adjust for variation in DNA quantity analyzed. Community similarity matrices were derived using the Bray-Curtis dissimilarity metric, a commonly used metric to compare microbial communities (Legendre and Legendre 1998, Horner-Devine et al. 2004, Yannarell and Triplett 2005, Fierer et al. 2007, Smith et al. 2010). Microbial communities were first visualized using an unconstrained non-metric multidimensional scaling (NMDS) ordination of community similarity, where more similar communities are closer in ordination space. I performed a permutational multivariate analysis of variance using distance matrices (ADONIS) to assess the contribution of environment and till categories to generating community similarity.

I applied canonical correspondence analysis (CCA) to further assess how till categories or specific environmental variables influenced community structure. Using CCA I was able to identify linear combinations of geochemical explanatory variables explaining variability in the multivariate community response (Legendre and Legendre 1998). CCA partitions total variance (inertia) into proportions explained by constraining variables with unadjusted proportions (equivalent to R^2) (Borcard et al. 2011). Using three successive CCAs, I was able to partition variance in community composition due to geochemical variables or till factor as described in

Borcard et al. (2011). I used a partial CCA to confirm the unadjusted variance partitioning calculated from the three separate CCA with glacial till category as a covariable. The explanatory variables that described the most influential T-RFLP gradients were selected using forward selection for each CCA separately (Borcard et al. 2011).

I further applied partial Mantel tests to compare the influence of geochemistry, geographic distance, and till factor on the composition of microbial communities because the tills are not randomly distributed in space, and geographic distance alone can indicate potentially genetically isolated and distinct communities (Horner-Devine et al. 2004, Martiny et al. 2006). The microbial community similarity matrix was calculated using the Bray-Curtis dissimilarity metric and geographic distance calculated based on Euclidean distance between sites (Legendre and Legendre 1998, Borcard et al. 2011). Environmental similarity was based on Euclidean distance of a select set of environmental variables, chosen to maximize the correlation with the community composition response (Clarke and Ainsworth 1993, Horner-Devine et al. 2004). In order to assess the influence of glacial tills, I coded these as dummy variables for each site (Legendre and Legendre 1998, Borcard et al. 2011).

Partial Mantel tests were also used to test the influence of community composition on enzyme activity of all four enzymes while controlling for the effect of site geochemistry and vice versa. Environmental variables were selected similar to above and enzyme activity similarity was calculated as Euclidean distance. All statistics were calculated in R with the "vegan" package using the following functions: "metaMDS" for NMDS ordination, "adonis" for analysis of variance using distance matrices "cca" for CCA and partial CCA, "ordistep" for CCA variable selection, and "anova" for permutational tests of CCA significance, "mantel" for partial Mantel tests, and "bioenv" for environmental variable selection for partial Mantel tests (Borcard et al. 2011, Oksanen et al. 2011).

RESULTS

Edaphic Characteristics

All soil geochemistry varied significantly across the four different glacial tills, with the exception of nitrate and TIN (Table 2). Phosphate levels varied across till categories ($F = 12.91$, $p < 0.0001$) with significantly higher concentration in the Ross till (1.33 mg PO_4 kg^{-1} dry soil) compared to all other tills (0.51 mg PO_4 kg^{-1} dry soil, $p < 0.0001$). SOC and TN were significantly influenced by till category ($F = 11.86$, $p < 0.0001$; $F = 16.46$, $p < 0.0001$, respectively) with significantly higher concentrations found in Taylor IV (0.53 g C kg^{-1} dry soil, 0.07 g N kg^{-1} dry soil, respectively) compared to all other tills (0.41 g C kg^{-1} dry soil, 0.05 g N kg^{-1} dry soil, respectively). Microbial biomass was significantly influenced by till ($F = 7.96$, $p = 0.0001$) with the lowest values occurring in the Taylor II till (2.18 mg microbial biomass C kg^{-1} dry soil) compared to all other tills, which averaged 4.18 mg microbial biomass C kg^{-1} dry soil. Ammonium levels were significantly different among tills ($F = 3.29$, $p = 0.027$), however the data did not follow a normal distribution, and the range of ammonium values was greatest in Taylor IV samples (0.056-2.14, mean = 0.23 mg N kg^{-1} dry soil) and much less variable in all other tills (0.032-0.49, mean = 0.093 mg N kg^{-1} dry soil). Soil pH and electrical conductivity differed significantly among tills ($F = 50.60$, $p < 0.0001$; $F = 10.84$, $p < 0.0001$, respectively) and were both highest in Taylor II (8.98 and 183.43 uS cm^{-1}, respectively) and lowest in Taylor IV (7.85 and 53.16 uS cm^{-1}, respectively). Water also significantly varied among tills ($F = 5.93$, $p = 0.0013$), reflecting a bimodal distribution, consistent with the selection of wet and dry sites.

Contemporary environmental variation (i.e. wet or dry sites) contributed to variation in physical soil variables: soil water content ($F = 743.54$, $p < 0.0001$), pH ($F = 157.29$, $p < 0.0001$), electrical conductivity ($F = 105.80$, $p < 0.0001$) and ammonium ($F = 6.91$, $p = 0.0109$), but no other geochemical parameters (Table 3). Percent soil moisture ranged nearly an order of magnitude within environmental categories: dry sites ranged from 0.19-1.66% and wet sites from 2.03-19.03%.

Microbial Community Structure

Bacterial OTU richness was not significantly different among tills but did vary between wet (mean = 70.66) and dry (mean = 58.42) environments ($F = 26.01$, $p < 0.0001$) with overall average richness of 64.72 across all sites (Table 3). Shannon diversity was also different among environments ($F = 31.65$, $p < 0.0001$) with a significant interaction between till and environment ($F = 3.90$, $p = 0.013$). NMDS ordination of microbial community similarity (stress = 0.204) showed that communities clustered by environment with overlapping confidence intervals among tills (Fig. 3). Both till and environment explained significant ($p < 0.001$) portions of the variation in community similarity (Table 4; $F = 3.79$, $r^2 = 0.12$; $F = 12.96$, $r^2 = 0.14$, respectively).

I used a sequence of CCA to examine relationships among community structure (T-RFLP profile similarity) and soil properties to assess how till categories and/or specific environmental variables influenced community structure (Fig. 4, Table 5). The first CCA model was significant ($p = 0.001$) and included water, pH, microbial biomass, phosphate, ammonium, nitrate, and electrical conductivity, and explained 48.9% of the explained T-RFLP-environment relationship in the first two axes (Fig. 4, Table 5). The second CCA model was significant ($p = 0.001$) and included only till category in the explanatory data matrix, explaining 75.3% of the model-explained T-RFLP-environment relationship in the first two axes. The third CCA model was significant ($p = 0.001$) and included pH, NH_4, NO_3, PO_4, EC and Till category, explaining 44.8% of the model-explained T-RFLP-environment relationship in the first two axes. Tills were responsible for only 3.4% of the total inertia (variance in community composition), while geochemical variables explained 18.5% of the variability. These results were confirmed with the partial CCA showing that soil properties were the main explanatory variables driving observed variation in microbial community structure, regardless of whether these soil properties varied with till or wet/dry environments (Fig. 4, Table 5).

Environmental similarity was calculated using only water, electrical conductivity, and pH to maximize the correlation between community composition and geochemical variables. Partial Mantel tests demonstrated community similarity was most strongly related to environmental similarity when controlled for geographic distance ($r = 0.55$, $p = 0.0001$) and till category ($r = 0.55$, $p = 0.0001$) (Table 7). However, it was also significantly correlated to geographic distance when controlled for environmental similarity ($r = 0.090$, $p = 0.0005$). Community similarity was

significantly, albeit weakly, related to till category when controlled for geographic distance ($r = 0.068$, $p = 0.0038$) or environmental similarity ($r = 0.087$, $p = 0.0038$). Differences among wet and dry sites were apparent as geographic distance and till were strongly related to wet site community similarity ($r = 0.41$, $p = 0.0001$; $r = 0.322$, $p = 0.0001$, respectively), but dry sites were not (0.075, $p = 0.031$; $r = 0.036$, $p = 0.164$, respectively).

Extracellular Enzyme Activity

Enzyme activity of AG, BG, and AP differed only among till categories while LAP activity differed only by hydrologic condition (Table 6). I ran multiple linear regressions on edaphic characteristics to determine which edaphic variables best described the activity of each enzyme (Table 8). All models were significant. The AG model (adj. $r^2 = 0.36$, $p < 0.0001$) included NH_4 ($t = 4.17$, $p < 0.0001$), PO_4 ($t = -3.86$, $p = 0.0003$), and EC ($t = 2.66$, $p = 0.0099$). The BG model (adj. $r^2 = 0.34$, $p < 0.0001$) included NH_4 ($t = 2.26$, $p = 0.0274$), NO_3 ($t = 2.36$, $p = 0.0213$), PO_4 ($t = -3.39$, $p = 0.0012$), and microbial biomass ($t = 3.02$, $p = 0.0037$). The LAP model (adj. $r^2 = 0.58$, $p = < 0.0001$) includes TOC ($t = -5.47$, $p < 0.0001$), microbial biomass ($t = 5.12$, $p < 0.0001$), and water ($t = -7.15$, $p < 0.0001$). The AP model (adj. $r^2 = 0.60$, $p < 0.0001$) included NH_4 ($t = 3.78$, $p = 0.0003$), PO_4 ($t = -3.93$, $p = 0.0002$), microbial biomass ($t = 2.73$, $p = 0.0082$), pH ($t = -4.07$, $p = 0.0001$), and water ($t = -3.73$, $p = 0.0004$).

Environmental similarity was calculated using water, microbial biomass, PO_4, and NH_4 to maximize the correlation between community composition and geochemical variables. Overall enzyme activity of each site was evaluated for a relationship between community similarity and environmental similarity using partial Mantel tests (Table 7). Overall enzyme activity was significantly related to both environment ($r = 0.14$, $p = 0.0001$) and community similarity ($r = 0.1302$, $p = 0.0078$). Dissimilarity among wet sites communities increased with distance ($r = 0.41$, $p = 0.0001$) as well as among dry sites, but with a much weaker relationship in dry sites ($r = 0.08$, $p = 0.0313$).

DISCUSSION

Microbial Community Structure

Microbial community structure was influenced by both historical factors (i.e. glacial till sequence) and contemporary environmental conditions (i.e. wet vs. dry) as illustrated by NMDS ordination and ADONIS analysis (Fig 3, Table 4). However, CCA revealed that environmental factors contributed to a larger proportion of the variability in community composition than till category (Table 5). Partial CCA (controlling for till effect) revealed only a slight change in the community composition arrangement, enhancing the separation of wet and dry sites, and demonstrating that the geochemical differences among tills were driving variation in microbial communities (Fig. 4 c, d). Environmental and till categories each explained a similar amount of variability in community composition (Table 4). This suggests that including environmental variables that differed among tills as well as local environments was important to accounting for observed variation in community composition. Partial Mantel tests show that environmental variables explain a much higher portion of the variability in composition than simple till category alone (Fig 4, Table 7). These three analyses suggest that contemporary environments and glacial history are significant influences on microbial community composition, however contemporary environmental factors, especially those associated with water availability, are driving more of the observed variability. Although many of the geochemical variables were associated with till category (Table 2), microbial populations are selected largely based on these contemporary environmental differences.

These data demonstrate the need to understand the role of not only the environmental drivers of community composition, but also the controlling factors, for example geological legacies versus contemporary hydrological processes. At local scales (< 1 km), previous studies have found environmental factors to be the significant driver of microbial community composition, whereas at regional scales (> 10,000 km) historical separation by geographic distance has a more significant influence (Martiny et al. 2006). Studies carried out at intermediate scales (10-3000 km) are the most likely to show a significant effect of both history and contemporary environment (Martiny et al. 2006). Taylor Valley is only about 30 km long and sampling sites are, at the greatest distance, about 21.5 km apart, putting this study at the low

end of the "intermediate" scaling. This may predict a greater importance of contemporary environmental factors, even given the pronounced differences in till chemistry (Burkins et al. 2000, Bockheim et al. 2008, Bate et al. 2008). However, investigations of invertebrate and microbial communities made at considerably broader scales in Victoria Land, Antarctica, have come to similar conclusions about the importance of local environmental drivers of soil communities (Barrett et al. 2006).

The harsh physical environment of the McMurdo Dry Valleys likely contributed to the differences in community composition in my study. In both ordination techniques, the first axis was related to water content of the soil indicating that the presence of water and the geochemical transformations associated with the rehydration and movement of solutes provide the majority of this environmental filter. Wet sites exhibited higher richness and diversity, and partial Mantel tests show that among wet sites, spatial proximity is a strong predictor of community similarity (Table 7, $r = 0.41$, $p = 0.0001$) while community similarity did not vary with geographic distance in dry sites ($r = 0.07$, $p = 0.0313$), suggesting increased homogeneity among dry surfaces relative to wet environments. Topographic position may help explain this pattern: wet sites considered in this study are located in topographic depressions as compared to dry sites typically located at the top of rises in the landscape. Flowpath depressions provide sheltered areas for snow, sediment, and biota to accumulate during winter high wind events, while dry sites were located on top of small rises, which are subject to wind-scour and aeolian movement of soils and associated organisms (Gooseff et al. 2003, Nkem et al. 2006b, Levy et al. 2011, Sabacka et al. 2012). The snow and sediment accumulation each winter could provide a cap on the previous years' biota and prevent dispersal during the winter season when most of the sediment and snow is transported (Nylen 2004). Analogous to microbial systems, plant dispersal studies have documented the effects of topography on seed dispersal, showing that seeds dispersed from hilltops disperse much further than seeds released from the bottom of hills (Katul and Poggi 2012). The apparent homogeneity among dry sites could be related to the topographic position of these sites which facilitates broader connectivity in the valley, while wet sites are more isolated. Additionally, till sequence is significantly related to the community similarity of wet sites, when corrected for geographic distance, but is not significant for dry sites (Table 7). That is, wet sites within the same till were more similar than dry sites within the same till, suggesting a different trajectory of community development in wet and dry soils. Wet sites may not be as well

connected across the landscape and thus allow for unique community dynamics in a particular site over time, especially considering that these are more favorable sites for biotic activity and reproduction compared to dry sites. Zeglin et al. (2011) also found that bacterial communities from dry sediments from distant regions within Wright Valley of the McMurdo Dry Valleys were more similar to each other than to local communities from within wetted stream margins. That study suggested a dispersal mechanism by which species from aquatic and terrestrial environments have different source pools. I hypothesize that in my sites the species pools are not necessarily different but rather topographic position affects the connectivity among landscape positions and drives the observed community similarity patterns.

Zhou et al. (2002) proposed that water availability can also drive spatial isolation of soils through eliminating competition as a driver of composition. That is, in wetter soils or during periods of episodic increased in moisture (i.e. rainfall or in active meltwater flowpaths), soil particles are connected via saturated pores and the exchange of nutrients and biota is facilitated allowing for well adapted species to successfully reproduce. The biogeochemical differences among our tills could drive differentiation and selection of communities in wet sites as these environmental factors may become more important with active populations constrained by resource competition. While in dry soils the particles are isolated and allow for more species to exist and increased probability of successful colonization because of reduced competition, however their population size will remain low as resources are scarce and not evenly distributed. TFRLP only reflects more abundant bacterial populations, and the elevated richness of wet sites could be a consequence of more suitable habitat and thus greater abundances of many populations in wet sites and not representative of true diversity.

Arid soil surfaces of the McMurdo Dry Valleys, which are unlikely to receive seasonal wetting from meltwater flowpaths, have been predicted to be repositories for DNA that has collected over time from cosmopolitan organisms but are possibly not active, analogous to a "seed bank" (Takacs-Vesbach et al. 2010, Lennon and Jones 2011). Theoretically, if dry sites represented the collective "seed bank" for all species within a till of Taylor Valley, the species richness would be greatest in dry sites and wet sites would simply be representative of a subset of species from this pool. Furthermore, dry sites with soil moisture <2% have been found to have 20-80% of nematodes in a dehydrated, ametabolic state (i.e. anhydrobiosis) and bacterial dormancy may follow similar patterns (Treonis and Wall 2005). Taxonomic assessments of

composition through "deep sequencing" methods may be necessary to elucidate patterns of total diversity. Future work should examine the composition of both active and dormant communities through DNA and RNA analyses to examine the importance of dormant individuals to maintaining diversity in these soils

Ecosystem Function

Inorganic N and P and microbial biomass were the most significant factors in determining enzyme activity (Table 8). Ammonium was the most common geochemical predictor of enzyme activity for the following variables AG, BG, AP, BG:LAP, LAP:AP, BG:AG. Elevated ammonium levels in the Dry Valleys are indicative of biological activity because ammonium deposition in the region is low (Claridge and Campbell 1987), and therefore accumulation of ammonium must be due to mineralization of organic N (Barrett et al. 2002). The relationship between ammonium and LAP:AP and BG:AG was negative and to be expected because both enzymes in the denominator had a stronger positive response to ammonium than the numerator. It is therefore not surprising that microbial activity tracks ammonium concentration well for most enzymes. It is surprising, however, that LAP activity is not predicted by any nitrogen parameter because as an amino acid degrading enzyme LAP should contribute to N acquisition for microbes. LAP was instead most strongly correlated with SOC, microbial biomass, and soil water content, although LAP and SOC were negatively related. Zeglin et al. (2009) also found a negative LAP-SOM relationship and other physical parameters of the soil were included in the best model of LAP activity. In a global scale meta-analysis, Sinsabaugh et al. (2008) found that LAP activity was strongly pH dependent, indicating at the biochemical level, the enzyme is much more efficient at higher pH. This study's sites are high in pH, similar to other desert environments (Virginia and Wall 1999), but LAP is still strongly predicted by pH of the soil (Fig. 5). pH may not appear as a predictor of LAP in the multiple linear regression model because water content is included in the model and there is a strong water-pH dependence in the data.

Enzyme activity is an indicator of nutrient deficiency of the microbial community and therefore higher levels should be related to greater associated nutrient demand (Caldwell 2005, Sinsabaugh et al. 2008). Phosphate followed patterns similar to previous studies establishing

significantly higher levels in the Ross till compared to all other tills (Table 2; Blecker et al. 2006, Bate et al. 2008). These differences are largely driven by parent material of the tills and not necessarily related to weathering and biotic transformation of phosphorus predicted by classical P availability models over geologic time (i.e. Walker and Syers 1976; Bate et al. 2008). AP activity was negatively related to phosphate availability in the multiple linear regression and demonstrated a significant power relationship (Fig 6), indicating greater P deficiency in older tills (Table 2) and in agreement with previous work (Zeglin et al. 2009). Despite differences in TN and ammonium among tills, LAP activity was only significantly influenced by environmental category, likely due to the physical variable differences between wet and dry sites (Table 3).

SOC is limiting in the Dry Valleys (Burkins et al. 2000) yet was not a predictor for either BG or AG activity. This could be due to the long term stabilization of enzymes on soil particles, which would cause the assay to not represent contemporary biological activity (Caldwell 2005, Stursova and Sinsabaugh 2008). However, the ratio of BG:AG should provide an indicator of available carbon quality, with higher AG reflecting greater abundance of storage polysaccharides and higher BG reflecting greater abundance of structural carbon (Sinsabaugh et al. 2010). There is a significant relationship between SOC levels and BG:AG ratio (Fig. 7) and given that higher levels of SOC in Taylor Valley are coincident with more recalcitrant legacy carbon (Burkins et al. 2000, Barrett et al. 2005), the elevated BG:AG activity suggests changes in carbon quality affect microbial activity.

Community Structure and Function

Contemporary environmental conditions along with community structure were significantly related to enzymatic metrics of ecosystem functioning. Partial Mantel tests revealed significant relationships and similar r values describing the influence of pH, electrical conductivity and water content on extracellular enzyme activity (Table 7). This suggests that both environment and community variables are important in determining potential enzyme activity of these soils. However, when dry sites were examined separately, community similarity did not predict similarity in enzymatic function, while in wet sites there was a significant relationship. These extracellular enzymes are broadly utilized across microbial taxa and therefore

may not be sensitive to compositional differences (Schimel 1995). However, I show that even these broad processes are related to composition of soil communities as indicated by T-RFLP profiles. T-RFLP characterizes the most abundant organisms present and which are most likely to contribute to these broad functions. Dry sites do not appear to reflect currently active microbial populations and may indicate the presence of enzyme stabilized on the soil surface (Stursova and Sinsabaugh 2008). The characterization of active and dormant populations in these different environments could further help illustrate the importance of each subset to ecosystem functions.

Connecting community composition to ecological functions such as enzyme activity, respiration, decomposition, and nitrogen cycling has been demonstrated by many previous studies (Cavigelli and Robertson 2000, Waldrop et al. 2001, Bell et al. 2005, Reed and Martiny 2007, Strickland et al. 2009, Boucher and Debroas 2009). For example, Boucher and Debroas (2009) demonstrated that specific T-RFLP fragments were associated with changes in enzyme activity, indicating that composition and population shifts in the community were related to changes in enzyme activity. However, Allison et al. (2007) found that the shift to more fungal dominated soils in the older soils of a chronosequence was not enough to compensate for nutrient limitation as exhibited by a negative relationship between enzyme activity and nutrient availability. Similarly in this study, enzyme activity analysis did not show that shifts in community composition were associated with changes in nutrient limitation. This study's connection between microbial community structure and ecosystem functioning is especially notable because they link broad ecological processes that are mediated by broad taxonomic groups of microbes, which theoretically may be less sensitive to shifts in composition (Schimel 1995). My data demonstrate that spatial variation in microbial communities, which are largely controlled by geochemical variation from historical legacies and contemporary processes, influence broad ecosystem functions.

CONCLUSIONS

The ultimate drivers of biogeography are processes including colonization, extinction, and speciation (Martiny et al. 2006), and this study demonstrates the potential for these processes to occur in microbial communities across sites separated by glacial history and fine-scale spatial variation due to topographic effects. Microbial community composition was significantly influenced by both till history and contemporary environmental conditions associated with geochemical differences among sites. However, environmental variables explained more variability in community similarity. Due to the well-documented dispersal of snow, sediment, and soil mesofauna during katabatic wind events it is unlikely that communities are assembled from multiple source pools. Instead, we propose that the major community shifts are due to the different topographic positions of wet and dry sites influencing the connectivity of microbial communities throughout Taylor Valley. Recent studies within the McMurdo Dry Valleys Long-Term Ecological Research project have sought to emphasize the potential importance of connectivity in desert ecosystems and this study contributes to these findings. Enzyme activity assays revealed nutrient limitation consistent with observed spatial patterns of ammonium and phosphate availability. The ratio of carbon acquiring enzymes reflected expected shifts in carbon quality associated with SOC availability. Environmental factors as well as microbial community composition had a significant influence on the overall enzyme activity among wet sites only, indicating the presence of currently active microbes. Together the environmental conditions and microbial community structure are influencing ecosystem functioning in these polar desert soils. Further analysis using "deep sequencing" methods may be necessary to fully elucidate patterns of biogeography associated with rare and low biomass bacterial taxa. In addition, I recommend that future studies examine the community structure of both active and inactive populations to understand how dormancy influences biogeography, reflects source pools, and relates to microbially-mediated functions.

FIGURES

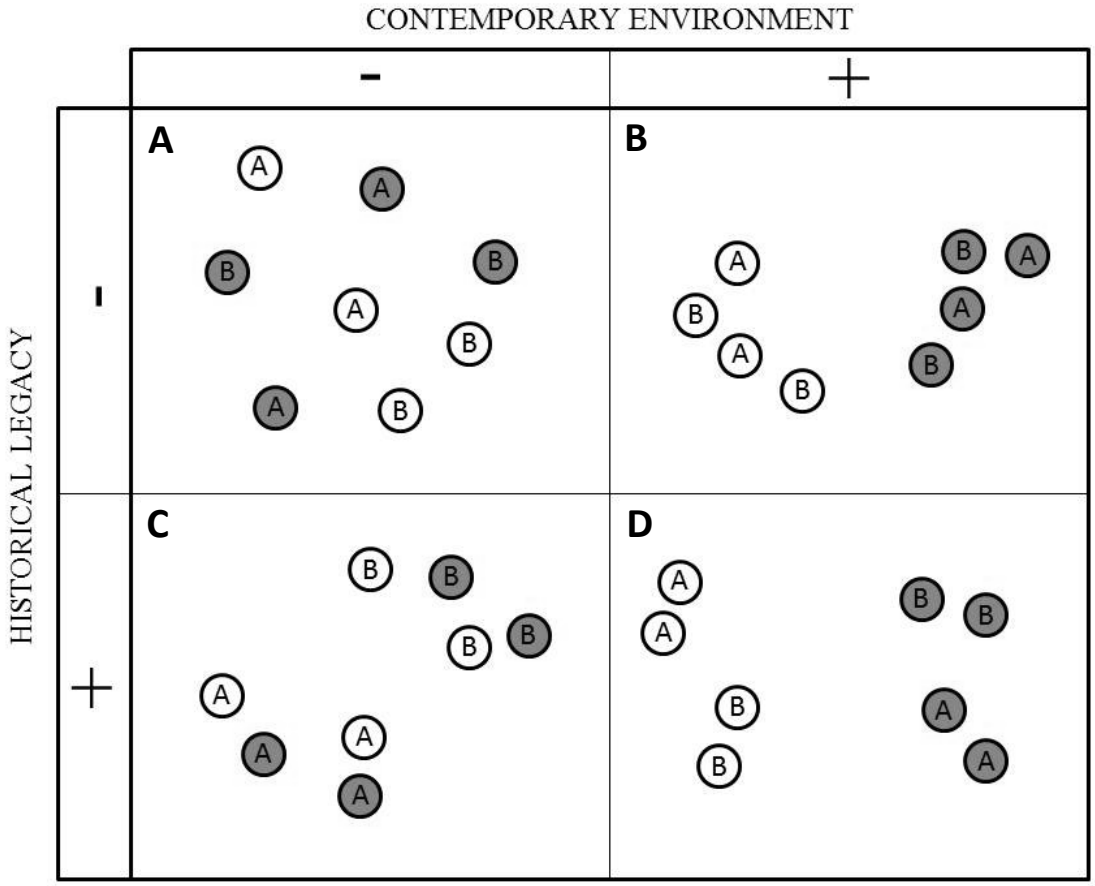

Figure 1. Theoretical community similarity ordinations from alternative hypotheses of microbial biogeography drivers as described by Martiny et al. (2006). White/grey circles represent sites with different environmental conditions; letters represent communities in historically separated sites. Panel a) displays random distribution of communities where there are no limits to species dispersal, b) Baas Becking's "everything is everywhere but the environment selects," c) only historical legacies drive community divergence, d) both historical legacy and contemporary environments select for the present communities.

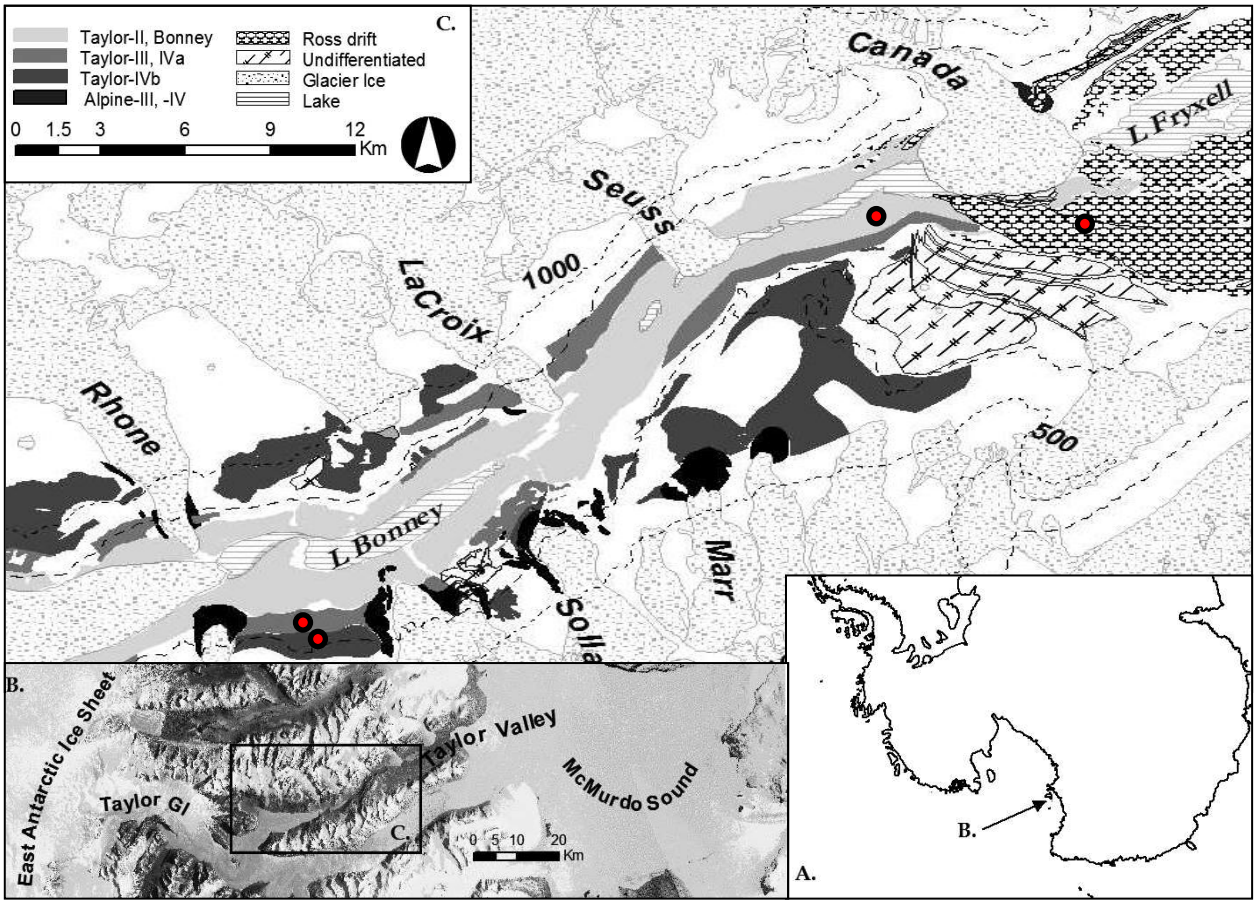

Figure 2. Major till units within Taylor Valley, Antarctica. Dots denote general sampling locations. Modified from Bockheim et al. (2008).

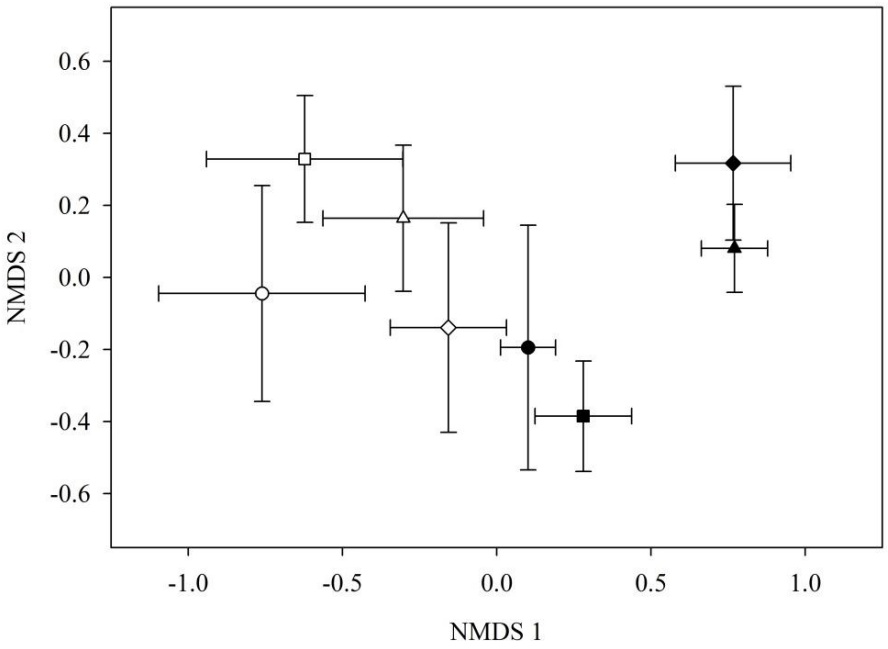

Figure 3. NMDS ordination of community similarity. Means plotted with 95% confidence intervals. Circle, Ross till; square, Taylor II, triangle, Taylor III; diamond, Taylor IV. Filled symbols are wet sites, open are dry sites.

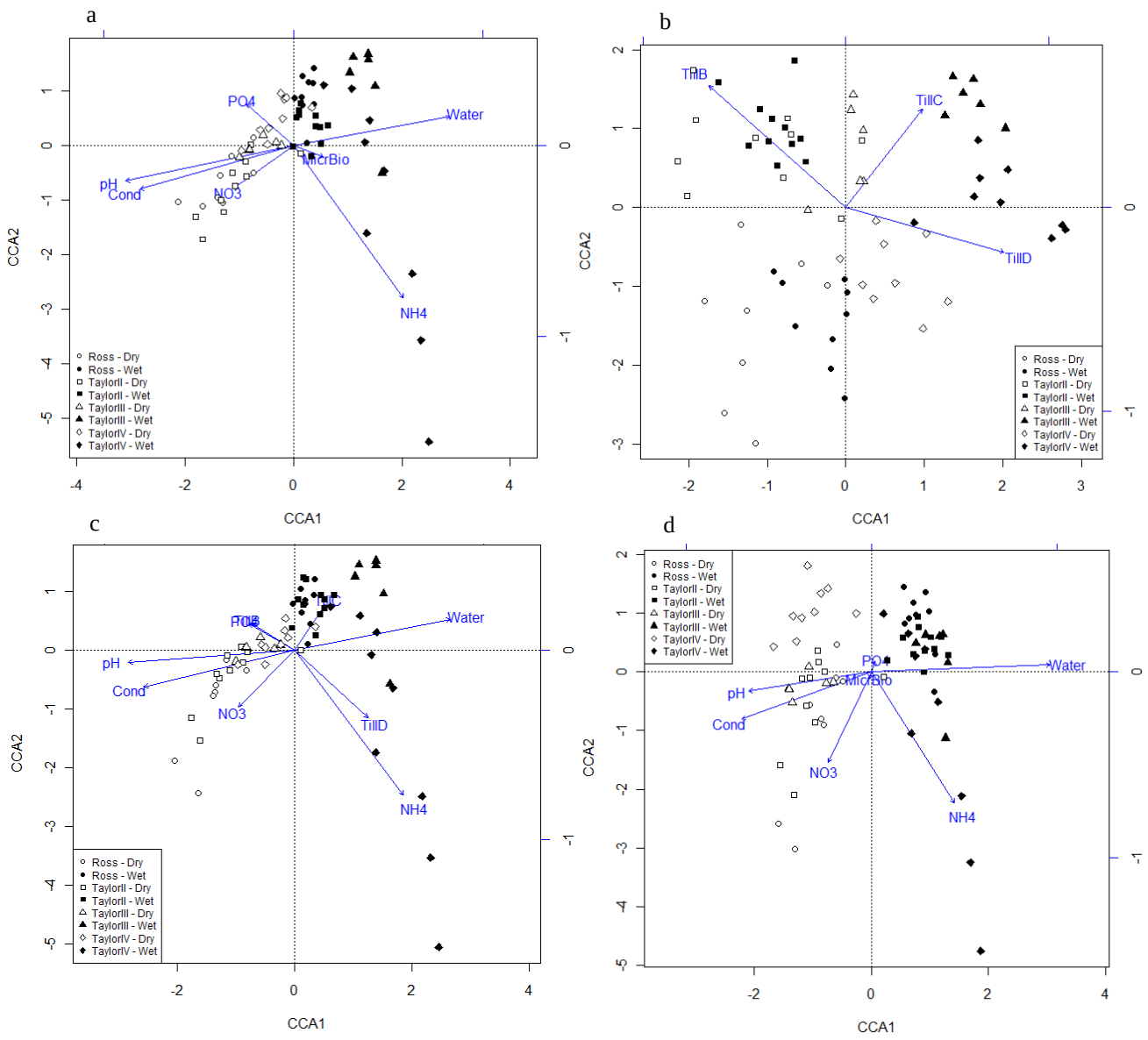

Figure 4. CCA of community similarity constrained by geochemical variables and/or till category. Points represent T-RFLP profiles and symbols indicate till (shape) or environment (color). Arrows represent geochemical variables showing the direction of increase in each variable and the length indicating the degree of correlation with the axes. a) is constrained by geochemical variables only. (b) is constrained by till factors, only 3 tills are displayed because factors are converted to dummy variables and only three dummy variables are needed to explain 4 levels of the till factor. (c) is constrained by both till factors and geochemical variables. (d) is a partial CCA constrained by geochemical variables while controlling for till factor.

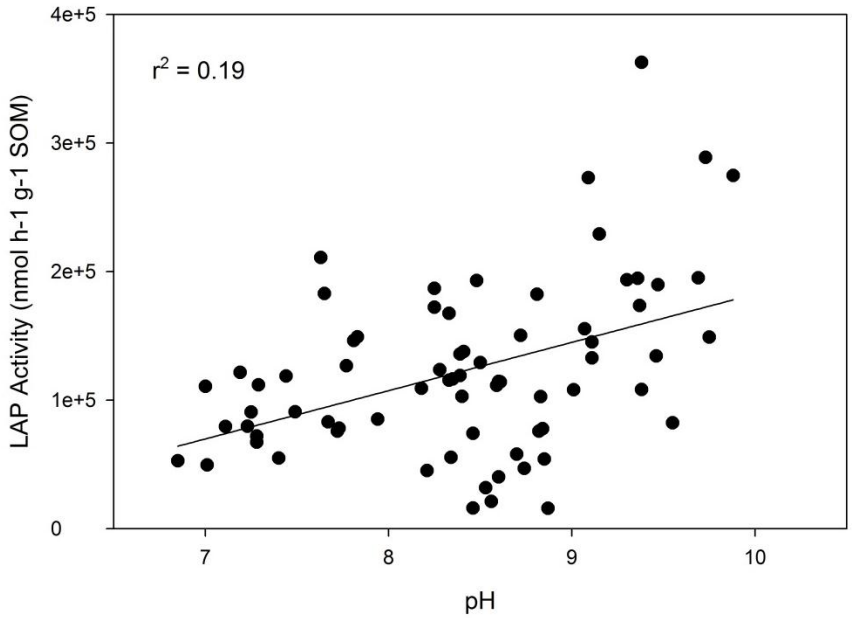

Figure 5. LAP activity regression as predicted by soil pH levels.

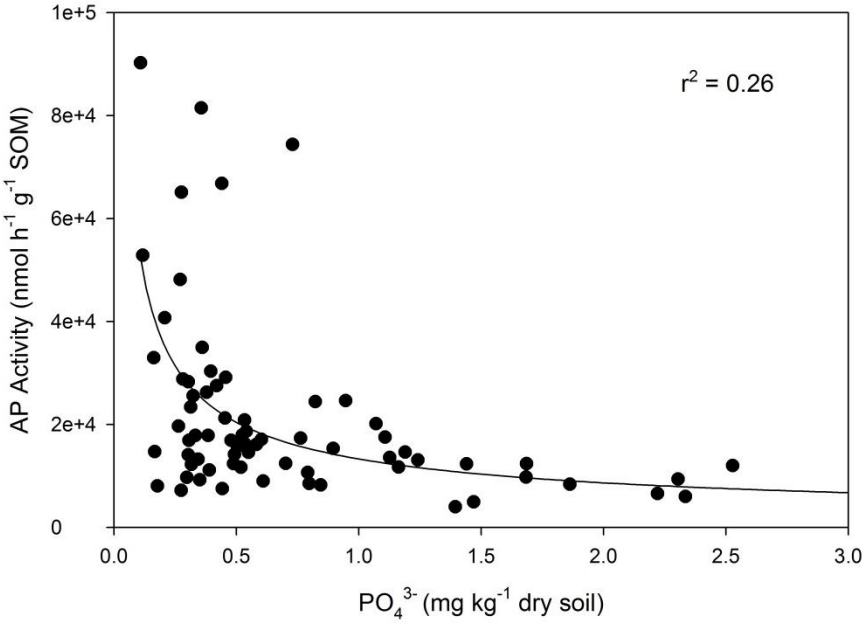

Figure 6. AP activity regression as predicted by soil phosphate concentrations.

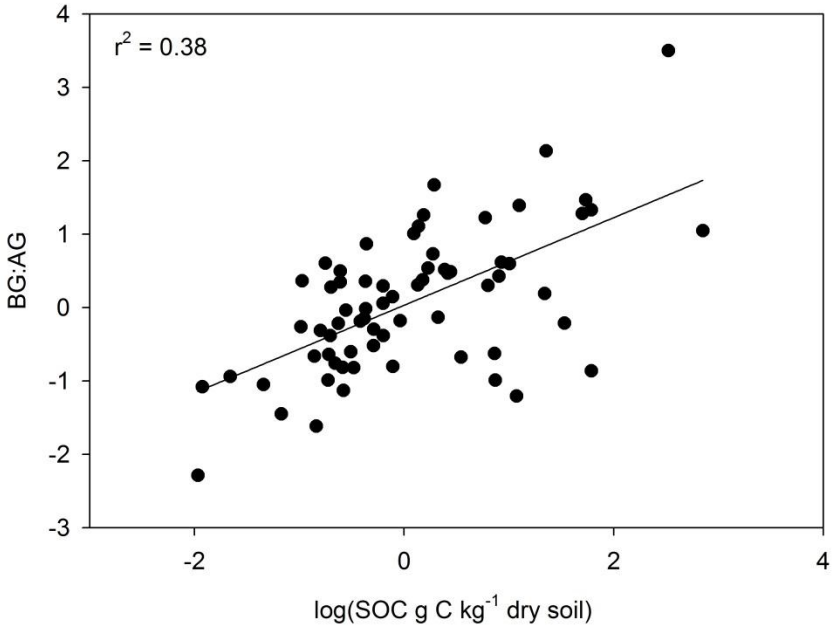

Figure 7. BG:AG activity ratio regression as predicted by SOC concentrations.

TABLES

Table 1. Taylor Valley, Antarctica glacial drift characteristics. Adapted from Bockheim et al. (2008).

Drift Unit	Approx. Age	Depth to Ice Cement (cm)	Weathering Stage[1]	Salt Stage[2]	Soil subgroup[3]
Ross Sea	12.4-23.8 ky	34	1.6	1.1	THt
Taylor II	113-120 ky	>45	2.1	1.2	Tao-Tat
Taylor III	208-375 ky	>85	2.7	2.0	Tao
Taylor IVa	1.6-2.1 My	>44	4.2	3.4	Tao-Sao
Taylor IVb	2.7-3.5 My	>46	4.0	2.8	TAo

[1] Weathering stages (reflects age of material based on boulder weathering and soil morphology; originally from Campbell and Claridge 1975)

1: fresh boulders; minimal horizon development; very shallow ice-cement; moderate patterned ground development

2: some boulder disintegration; weak horizon development; shallow ice-cement; strong patterned ground development

3: boulders with distinct rounding, some cavernous weathering and ventifacts; distinct horizon development; moderately deep soil depth

4: boulders reduced by ventifaction, crumbling; strongly developed cavernous weathering; very distinct soil horizons; deep soil profiles

5: few boulders; well developed desert pavement with extensive crumbling, rounding; very distinct soil horizons; deep soil profiles

6: weathered and crumbled bedrock; very distinct soil horizon development; shallow to deep profiles

[2] Salt stages (reflects soil age and related to electrical conductivity; Bockheim 1990, 2002)

0: no visible salts; <0.6 dS m^{-1}

1: salt coatings on bottom of stones; 0.6-5.0 dS m^{-1}

2: salt flecks 1-2 mm in diameter covering <20% of area of a horizon; 5.0-18 dS m^{-1}

3: salt flecks 1-2 mm in diameter covering >20% of area of a horizon; 18-25 dS m^{-1}

4: weakly cemented salt pan; 25-40 dS m^{-1}

5: strongly cemented salt pan; 40-60 dS m^{-1}

6: indurated salt pan; 60-100+ dS m^{-1}

[3] THt = Typic Haploturbel; TAt = Typic Anhyturbl; TAo = Typic Anhyorthel; SAo = Salic Anhyorthel

Table 2. Means ±SE of soil characteristics for each glacial till unit. Different letters indicate a significant difference among tills.

	Ross	Taylor II	Taylor III	Taylor IV
SOC (g C kg^{-1} dry soil)	0.38 ±0.03^{b}	0.30 ±0.03^{b}	0.40 ±0.04^{b}	0.53 ±0.04^{a}
TN (g N kg^{-1} dry soil)	0.05 ±0.004^{b}	0.04 ±0.003^{c}	0.05 ±0.004^{bc}	0.07 ±0.006^{a}
NH_4-N (mg N kg^{-1} dry soil)	0.077 ±0.009^{b}	0.097 ±0.019^{ab}	0.109 ±0.036^{ab}	0.288 ±0.119^{a}
NO_3-N (mg N kg^{-1} dry soil)	0.732 ±0.541	0.813 ±0.342	0.283 ±0.045	0.11 ±0.23
TIN (mg N kg^{-1} dry soil)	0.81 ±0.541	0.91 ±0.351	0.392 ±0.061	0.398 ±0.12
PO_4 (mg PO_4 kg^{-1} dry soil)	1.334 ±0.179^{a}	0.576 ±0.08^{b}	0.417 ±0.05^{b}	0.501 ±0.081^{b}
Microbial Biomass (mg C kg^{-1} dry soil)	3.612 ±0.399^{a}	2.179 ±0.279^{b}	3.388 ±0.503^{ab}	5.243 ±0.075^{a}

Table 3. Means ±SE of soil edaphic characteristics, richness, and Shannon diversity (H') for wet and dry environmental categories within each glacial till unit. (*) indicates a significant difference between wet and dry sites within a given till (one-way ANOVA within tills, *p < 0.05, **p < 0.01, p < 0.001, ****p <0.0001).

	Ross		Taylor II		Taylor III		Taylor IV	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Water (%)	0.903 ±0.183	13.022 ±1.614****	0.370 ±0.050	8.046 ±0.870****	0.348 ±0.066	9.807 ±1.210****	0.549 ±0.066	13.611 ±0.935****
pH	9.36 ±0.11	7.99 ±0.17****	9.29 ±0.13	8.70 ±0.04***	8.45 ±0.13	7.30 ±0.05****	8.38 ±0.10	7.32 ±0.12****
EC ($\mu S\ cm^{-1}$)	379.9 ±96.5	23.03 ±5.42****	295.4 ±147.6	81.6 ±10.7*	126.2 ±25.3	16.73 ±0.81****	89.7 ±20.7	16.67 ±2.63****
Richness	55.1 ±4.0	67.7 ±3.8*	58.2 ±2.5	78.6 ±2.4****	60.0 ±2.6	67.7 ±2.6	60.6 ±3.2	65.9 ±3.2
Diversity (H')	3.44 ±0.08	3.78 ±0.08**	3.50 ±0.05	3.91 ±0.05****	3.62 ±0.04	3.71 ±0.04	3.57 ±0.05	3.68 ± 0.05

Table 4. Influence of till and environmental categories from ADONIS. df, degrees of freedom; SS, sums of squares; MS, mean square. Tests are carried out with 9,999 permutations.

Factor	df	SS	MS	F Model	R^2	p
Till	3	2.252	0.751	3.793	0.118	0.0001
Environment	1	2.565	2.565	12.962	0.135	0.0001
Till x Environment	3	2.341	0.780	3.944	0.123	0.0001
Residuals	60	11.874	0.198		0.624	
Total	67	19.032			1.000	

Table 5. Influence of geochemical variables and till category from CCA. Constraining environmental variables were chosen using forward selection process. $\Sigma\lambda_i$ is the sum of constraining canonical eigenvalues. Total inertia is the sum of all eigenvalues ($\Sigma\lambda_i$/Total Inertia is the proportion of T-RFLP profiles explained by constraining variables). T-RFLP-evn (%) is the percent of the T-RFLP-env relationship ($\Sigma\lambda_i$) explained by the first two CCA axes. * indicates the variable partialled out.

Model	Constraining Variables	$\Sigma\lambda_i$	Total Inertia	T-RFLP-env (%)
Geochemical	pH, NH_4, water, NO_3, PO_4, EC, microbial biomass	1.270	5.434	48.9
Till	Till	0.451	5.434	75.3
Geochemical and Till	pH, NH_4, water, NO_3, PO_4, EC, microbial biomass, Till	1.542	5.434	41.7
Partial	pH, NH_4, water, NO_3, PO_4, EC, microbial biomass (Till*)	1.087	5.434	51.8

Table 6. Means ±SE of enzyme activity and enzyme ratios across tills. Alpha-glucosidase activity (AG, nmol h^{-1} g^{-1} OM); beta-glucosidase activity (BG, nmol h^{-1} g^{-1} OM); leucyl-aminopeptidase activity (LAP, nmol h^{-1} g^{-1} OM); alkaline phosphatase activity (AP, nmol h^{-1} g^{-1} OM). Letters indicate significant difference of means among tills ($p < 0.05$).

	Ross		Taylor II		Taylor III		Taylor IV	
AG	742	±53^{b}	1686	± 267^{a}	1860	± 273^{a}	1781	± 355^{a}
BG	842	±79^{a}	1435	± 197^{ab}	1853	± 273^{b}	1993	± 243^{b}
LAP	63753	±7176	67366	± 10625	62982	± 10574	50263	± 3695
AP	5194	±485^{a}	6482	± 598^{a}	13321	± 1844^{b}	15298	± 2231^{b}
BG:LAP	0.015	±0.002^{c}	0.029	± 0.004^{bc}	0.036	± 0.008^{ab}	0.046	± 0.007^{a}
BG:AP	0.178	± 0.021^{ab}	0.218	± 0.023^{a}	0.145	± 0.016^{ab}	0.147	± 0.014^{b}
LAP:AP	12.75	± 1.27^{a}	10.34	± 1.28^{a}	4.97	± 0.6^{b}	4.59	± 0.66^{b}
BG:AG	1.14	± 0.06^{ab}	0.9	± 0.04^{c}	1.02	± 0.04b^{c}	1.3	± 0.08^{a}

Table 7. Partial Mantel testing the influence of the geochemical environment, geographic distance, and till age on community similarity and extracellular enzyme activity (EEA). Pearson's r and p values after 9,999 permutations. *indicates significant effect ($p < 0.05$). "NA" indicates a Mantel test between the two other matrices. [1] indicates environmental similarity including variables pH, EC, and water content. [2] indicates environmental similarity including variables water, microbial biomass, PO_4, and NH_4. [3] indicates environmental similarity including all geochemical variables.

Response	Effect of:	Controlled for:	r	p
Community	Environment[1]	Distance	0.5509	0.0001*
Community	Environment[1]	Till	0.5544	0.0001*
Community	Distance	Environment[1]	0.08992	0.0005*
Community	Till	Distance	0.06786	0.0038*
Community	Till	Environment[1]	0.08683	0.0004*
Dry Site Community	Distance	Environment[1]	0.07527	0.0313*
Dry Site Community	Till	Distance	0.03608	0.1638
Wet Site Community	Distance	Environment[1]	0.4053	0.0001*
Wet Site Community	Till	Distance	0.322	0.0001*
EEA	Environment[2]	Community	0.14	0.0001*
EEA	Community	Environment[2]	0.1302	0.0078*
Dry Site EEA	Community	Environment[2]	0.09502	0.1136
Dry Site EEA	Environment[2]	Community	0.07825	0.1611
Wet Site EEA	Community	Environment[2]	0.3195	0.0001*
Wet Site EEA	Environment[2]	Community	0.4057	0.0007*
Environment[3]	Distance	----	0.1904	0.0001*

Table 8. Multiple linear regression results for enzyme assays and enzyme ratios. Alpha-glucosidase activity (AG, nmol h^{-1} g^{-1} OM); beta-glucosidase activity (BG, nmol h^{-1} g^{-1} OM); leucyl-aminopeptidase activity (LAP, nmol h^{-1} g^{-1} OM); alkaline phosphatase activity (AP, nmol h^{-1} g^{-1} OM).

Enzyme	Adj. R2	Model p-value	Variable	t-value	p-value
AG	0.358	< 0.0001	NH_4	4.17	<0.0001
			PO_4	-3.86	0.0003
			EC	2.66	0.0099
BG	0.342	<0.0001	NH_4	2.26	0.0274
			NO_3	2.36	0.0213
			PO_4	-3.39	0.0012
			Microbial biomass	3.02	0.0037
LAP	0.579	<0.0001	SOC	-5.47	<0.0001
			Microbial biomass	5.12	<0.0001
			Water content	-7.15	<0.0001
AP	0.604	<0.0001	NH_4	3.78	0.0003
			PO_4	-3.93	0.0002
			Microbial biomass	2.73	0.0082
			pH	-4.07	0.0001
			Water content	-3.73	0.0004
BG:LAP	0.423	<0.0001	NH_4	4.13	0.0001
			pH	-3.60	0.0006
BG:AP	0.168	0.0003	EC	3.81	0.0003
LAP:AP	0.619	<0.0001	SOC	-2.64	0.0103
			NH_4	-3.16	0.0024
			PO_4	2.38	0.0205
			pH	5.83	<0.0001
BG:AG	0.518	<0.0001	TN	8.31	<0.0001
			NH_4	-2.99	0.0039

REFERENCES

Allison, V., L. Condron, D. Peltzer, S. Richardson, and B. Turner. 2007. Changes in enzyme activities and soil microbial community composition along carbon and nutrient gradients at the Franz Josef chronosequence, New Zealand. Soil Biology and Biochemistry 39:1770-1781.

Baas Becking, L. 1934. Geobiologie of inleiding tot de milieukunde. W.P. Van Stockum & Zoon, The Hague, Netherlands.

Barrett, J. E., M. N. Gooseff, and C. Takacs-Vesbach. 2009. Spatial variation in soil active-layer geochemistry across hydrologic margins in polar desert ecosystems. Hydrology and Earth System Sciences 13:2349-2358.

Barrett, J. E., M. A. Poage, M. N. Gooseff, and C. T. Vesbach. 2010. The legacy of aqueous environments on soils of the McMurdo Dry Valleys: contexts for future exploration of martian soils. pp. 78-109 *in* P. Doran, W. B. Lyons, and D. M. McKnight, eds. Life in Antarctic Deserts and Other Cold Dry Environments: Astrobiological Analogs. Cambridge University Press.

Barrett, J. E., R. A. Virginia, A. N. Parsons, and D. H. Wall. 2005. Potential soil organic matter turnover in Taylor Valley, Antarctica. Arctic, Antarctic, and Alpine Research 37:108-117.

Barrett, J. E., R. A. Virginia, D. H. Wall, S. C. Cary, B. J. Adams, A. L. Hacker, and J. M. Aislabie. 2006. Co-variation in soil biodiversity and biogeochemistry in northern and southern Victoria Land, Antarctica. Antarctic Science 18:535.

Barrett, J. E., R. A. Virginia, D. H. Wall, P. T. Doran, A. G. Fountain, K. A. Welch, and W. B. Lyons. 2008. Persistent effects of a discrete warming event on a polar desert ecosystem. Global Change Biology 14:2249-2261.

Barrett, J. E., R. A. Virginia, D. H. Wall, A. N. Parsons, L. E. Powers, and M. B. Burkins. 2004. Variation in biogeochemistry and soil biodiversity across spatial scales in a polar desert ecosystem. Ecology 85:3105-3118.

Barrett, J. E., R. A. Virginia, and D. H. Wall. 2002. Trends in resin and KCl-extractable soil nitrogen across landscape gradients in Taylor Valley, Antarctica. Ecosystems 5:289-299.

Barrett, J. E., R. A. Virginia, W. Lyons, D. McKnight, J. Priscu, P. Doran, A. Fountain, D. H. Wall, and D. Moorhead. 2007. Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. Journal of Geophysical Research 112.

Bate, D. B., J. E. Barrett, M. A. Poage, and R. A. Virginia. 2008. Soil phosphorus cycling in an Antarctic polar desert. Geoderma 144:21-31.

Bell, T., J. A. Newman, B. W. Silverman, S. L. Turner, and A. K. Lilley. 2005. The contribution of species richness and composition to bacterial services. Nature 436:1157-1160.

Billings, W. 1985. The historical development of physiological plant ecology. pp. 1-15 *in* B. Chabot and H. Mooney, eds. Physiological Ecology of North American Plants. Springer.

Blecker, S. W., J. A. Ippolito, J. E. Barrett, D. H. Wall, R. A. Virginia, and K. L. Norvell. 2006. Phosphorus fractions in soils of Taylor Valley, Antarctica. Soil Science Society of America Journal 70:806-815.

Bockheim, J. G. 1997. Properties and classification of cold desert soils from Antarctica. Soil Science Society of America Journal 61:224-231.

Bockheim, J. G. 2002. Landform and soil development in the McMurdo Dry Valleys, Antarctica: A regional synthesis. Arctic, Antarctic, and Alpine Research2 34:308-317.

Bockheim, J. G., M. L. Prentice, and M. Mcleod. 2008. Distribution of glacial deposits, soils, and permafrost in Taylor Valley, Antarctica. Arctic, Antarctic, and Alpine Research 40:279-286.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, New York, NY.

Boucher, D., and D. Debroas. 2009. Impact of environmental factors on couplings between bacterial community composition and ectoenzymatic activities in a lacustrine ecosystem. FEMS Microbiology Ecology 70:66-78.

Broadbent, F. E. 1953. The soil organic fraction. Advances in Agronomy 5:153-183.

Buckley, D. H., and T. M. Schmidt. 2003. Diversity and dynamics of microbial communities in soils from agro-ecosystems. Environmental Microbiology 5:441-52.

Burkins, M. B., R. A. Virginia, C. P. Chamberlain, and W. D. H. 2000. Origin and distribution of soil organic matter in Taylor Valley, Antarctica. Ecology 81:2377-2391.

Caldwell, B. 2005. Enzyme activities as a component of soil biodiversity: A review. Pedobiologia 49:637-644.

Casamayor, E. O., R. Massana, S. Benlloch, L. Øvreås, B. Díez, V. J. Goddard, J. M. Gasol, I. Joint, F. Rodríguez-Valera, and C. Pedrós-Alió. 2002. Changes in archaeal, bacterial and eukaryal assemblages along a salinity gradient by comparison of genetic fingerprinting methods in a multipond solar saltern. Environmental Microbiology 4:338-48.

Cavigelli, M. A., and G. P. Robertson. 2000. The functional significance of denitrifier community composition in a terrestrial ecosystem. Ecology 81:1402-1414.

Cheng, W., and R. A. Virginia. 1993. Measurement of microbial biomass in Arctic tundra soils using fumigation-extraction and substrate-induced respiration procedures. Soil Biology and Biochemistry 25:135-141.

Claridge, G., and I. Campbell. 1987. Antarctica: soils, weathering processes and environment. Developments in Soil Science 16. Elsevier Press, Amsterdam.

Clarke, K., and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92:205-219.

Courtright, E. M., D. H. Wall, and R. A. Virginia. 2001. Determining habitat suitability for soil invertebrates in an extreme environment: the McMurdo Dry Valleys, Antarctica. Antarctic Science 13:9-17.

Cross, A. F., and W. H. Schlesinger. 2001. Biological and geochemical controls on phosphorus fractions in semiarid soils. Biogeochemistry 52:155-172.

Crump, B. C., C. S. Hopkinson, M. L. Sogin, and J. E. Hobbie. 2004. Microbial biogeography along an estuarine salinity gradient : combined influences of bacterial growth and residence time. Applied and Environmental Microbiology 70:1494-1505.

Denton, G., R. Armstrong, and M. Stuiver. 1971. The late Cenozoic glacial history of Antarctica. pp. 276-306 *in* K. Turekian, ed. The Late Cenozoic glacial ages. Yale University Press, New Haven.

Denton, G., J. G. Bockheim, S. Wilson, and M. Stuiver. 1989. Late Wisconsin and Early Holocene Glacial History , Inner Ross Embayment, Antarctica. Quaternary Research 31:151-182.

Doran, P. T. 2002. Valley floor climate observations from the McMurdo dry valleys, Antarctica, 1986–2000. Journal of Geophysical Research 107.

Dunbar, J., L. O. Ticknor, and C. R. Kuske. 2001. Phylogenetic specificity and reproducibility and new method for analysis of terminal restriction fragment profiles of 16S rRNA genes from bacterial communities. Applied and Environmental Microbiology 67:190-197.

Esposito, R. M. M., S. L. Horn, D. M. McKnight, M. J. Cox, M. C. Grant, S. A. Spaulding, P. T. Doran, and K. D. Cozzetto. 2006. Antarctic climate cooling and response of diatoms in glacial meltwater streams. Geophysical Research Letters 33:2-5.

Fierer, N., J. L. Morse, S. T. Berthrong, E. S. Bernhardt, R. B. Jackson. 2007. Environmental controls on the landscape-scale biogeography of stream bacterial communities. Ecology 88:2162-2173.

Fierer, N., and R. B. Jackson. 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.

Fountain, A. G., W. B. Lyons, M. B. Burkins, G. L. Dana, P. T. Doran, K. J. Lewis, D. M. McKnight, D. L. Moorhead, A. N. Parsons, J. C. Priscu, D. H. Wall, R. A. J. Wharton, and R. A. Virginia. 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. BioScience 49:961-971.

Freckman, D. W., and R. A. Virginia. 1997. Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. Ecology 78:363-369.

Fritsen, C. H., A. M. Grue, and J. C. Priscu. 2000. Distribution of organic carbon and nitrogen in surface soils in the McMurdo Dry Valleys, Antarctica. Polar Biology 23:121-128.

Gooseff, M. N., J. E. Barrett, P. T. Doran, A. G. Fountain, W. B. Lyons, A. N. Parsons, D. L. Porazinska, R. A. Virginia, and D. H. Wall. 2003. Snow-Patch influence on soil biogeochemical processes and invertebrate distribution in the McMurdo Dry Valleys, Antarctica. Arctic, Antarctic, and Alpine Research 35:91-99.

Green, J. L., A. J. Holmes, M. Westoby, I. Oliver, D. Briscoe, M. Dangerfield, M. Gillings, and A. J. Beattie. 2004. Spatial scaling of microbial eukaryote diversity. Nature 432:747-750.

Green, J. L., and B. J. M. Bohannan. 2006. Spatial scaling of microbial biodiversity. Trends in ecology & evolution 21:501-507.

Hall, B. L., and G. H. Denton. 2000. Radiocarbon chronology of Ross Sea drift, eastern Taylor Valley, Antarctica: Evidence for a grounded ice sheet in the Ross Sea at the last glacial maximum. Geografiska Annaler 82:305-336.

Harris, K. J., A. E. Carey, W. B. Lyons, K. A. Welch, and A. G. Fountain. 2007. Solute and isotope geochemistry of subsurface ice melt seeps in Taylor Valley, Antarctica. Geological Society of America Bulletin 119:548-555.

Higgins, S. M., G. H. Denton, and C. H. Hendy. 2000a. Glacial geomorphology of Bonney Drift, Taylor Valley, Antarctica. Geografiska Annaler 82:365-389.

Higgins, S., C. Hendy, and G. Denton. 2000b. Geochronology of Bonney Drift, Taylor Valley, Antarctica: evidence for interglacial expansions of Taylor Glacier. Geografiska Annaler 82:391-409.

Horner-Devine, M. C., M. Lage, J. B. Hughes, and B. J. M. Bohannan. 2004. A taxa-area relationship for bacteria. Nature 432:750-753.

Katul, G. G., and D. Poggi. 2012. The effects of gentle topographic variation on dispersal kernels of inertial particles. Geophysical Research Letters 39.

Kennedy, A. D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. Arctic and Alpine Research 25:308-315.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier.

Lennon, J. T., and S. E. Jones. 2011. Microbial seed banks: the ecological and evolutionary implications of dormancy. Nature Reviews: Microbiology 9:119-130.

Levy, J. S., A. G. Fountain, M. N. Gooseff, K. A. Welch, and W. B. Lyons. 2011. Water tracks and permafrost in Taylor Valley, Antarctica: Extensive and shallow groundwater connectivity in a cold desert ecosystem. Geological Society of America Bulletin 123:2295-2311.

Liu, W. T., T. L. Marsh, H. Cheng, and L. J. Forney. 1997. Characterization of microbial diversity by determining terminal restriction fragment length polymorphisms of genes encoding 16S rRNA. Applied and Environmental Microbiology 63:4516-4522.

Lyons, W. B., A. Fountainy, P. Doranz, J. C. Priscux, K. Neumann, and K. A. Welch. 2000. Importance of landscape position and legacy: the evolution of the lakes in Taylor Valley , Antarctica. Freshwater Biology 43:355-367.

Lyons, W. B., K. A. Welch, A. E. Carey, P. T. Doran, D. H. Wall, R. A. Virginia, A. G. Fountain, C. M. Tremper, and B. M. Csatho. 2005. Groundwater seeps in Taylor Valley Antarctica: an example of a subsurface melt event. Annals Of Glaciology 40:200-206.

Martiny, J. B. H., B. J. M. Bohannan, J. H. Brown, R. K. Colwell, J. A. Fuhrman, J. L. Green, M. C. Horner-Devine, M. Kane, J. A. Krumins, C. R. Kuske, P. J. Morin, S. Naeem, L. Ovreas, A. Reysenbach, V. H. Smith, and J T. Staley. 2006. Microbial biogeography: putting microorganisms on the map. Nature Reviews: Microbiology 4:102-112.

Michalski, G., J. Bockheim, C. Kendall, and M. Thiemens. 2005. Isotopic composition of Antarctic Dry Valley nitrate: Implications for NOy sources and cycling in Antarctica. Geophysical Research Letters 32.

Mitchell, K. R., and C. D. Takacs-Vesbach. 2008. A comparison of methods for total community DNA preservation and extraction from various thermal environments. Journal of Industrial Microbiology and Biotechnology 35:1139-47.

Nelson, D. W., and L. E. Sommers. 1982. Total carbon, organic carbon, and organic matter. pp. 539-597 *in* A. L. Page, R. H. Miller, and D. R. Keeney, eds. Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, WI.

Nkem, J. N., R. A. Virginia, J. E. Barrett, D. H. Wall, and G. Li. 2006a. Salt tolerance and survival thresholds for two species of Antarctic soil nematodes. Polar Biology 29:643-651.

Nkem, J. N., D. H. Wall, R. A. Virginia, J. E. Barrett, E. J. Broos, D. L. Porazinska, and B. J. Adams. 2006b. Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. Polar Biology 29:346-352.

Nylen, T. H., A. G. Fountain, P. T. Doran. 2004. Climatology of katabatic winds in the McMurdo dry valleys, southern Victoria Land, Antarctica. Journal of Geophysical Research 109.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2011. Community ecology package (vegan).

Osborn, A., E. R. Moore, and K. N. Timmis. 2000. An evaluation of terminal-restriction fragment length polymorphism (T-RFLP) analysis for the study of microbial community structure and dynamics. Environmental Microbiology 2:39-50.

Ovreas, L., L. Forney, D. F. L, and V. Torsvik. 1997. Distribution of bacterioplankton in meromictic Lake Saelenvannet , as determined by denaturing gradient gel electrophoresis of PCR-amplified gene fragments coding for 16S rRNA. Applied and Environmental Microbiology 63:3367-3373.

Poage, M. A., J. E. Barrett, R. A. Virginia, and D. H. Wall. 2008. The influence of soil geochemistry on nematode distribution, McMurdo Dry Valleys, Antarctica 40:119-128.

Priscu, J. C. 1995. Phytoplankton nutrient deficiency in lakes of the McMurdo dry valleys, Antarctica. Freshwater Biology 34:215-227.

Reed, H. E., and J. B. H. Martiny. 2007. Testing the functional significance of microbial composition in natural communities. FEMS Microbiology Ecology 62:161-70.

Sabacka, M., J. C. Priscu, H. J. Basagic, A. G. Fountain, D. H. Wall, R. A. Virginia, and M. C. Greenwood. 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. Geomorphology.

Schimel, J. 1995. Ecosystem consequences of microbial diversity and community structure. pp. 239-254 *in* F. S. Chapin and C. Korner, eds. Arctic and Alpine Biodiversity: patterns, causes, and ecosystem consequences. Springer-Verlag, Berlin.

Sinsabaugh, R. L., D. J. Van Horn, J. J. F. Shah, and S. Findlay. 2010. Ecoenzymatic stoichiometry in relation to productivity for freshwater biofilm and plankton communities. Microbial Ecology 60:885-893.

Sinsabaugh, R. L., C. L. Lauber, M. N. Weintraub, B. Ahmed, S. D. Allison, C. Crenshaw, A. R. Contosta, D. Cusack, S. Frey, M. E. Gallo, T. B. Gartner, S. E. Hobbie, K. Holland, B. L. Keeler, J. S. Powers, M. Stursova, C. Takacs-Vesbach, M. P. Waldrop, M. D. Wallenstein, D. R. Zak, and L. H. Zeglin. 2008. Stoichiometry of soil enzyme activity at global scale. Ecology Letters 11:1252-1264.

Smith, J. L., J. E. Barrett, G. Tusnády, L. Rejtö, and S. C. Cary. 2010. Resolving environmental drivers of microbial community structure in Antarctic soils. Antarctic Science 22:673-680.

Staddon, W. J., and J. T. Trevors. 1998. Soil microbial diversity and community structure across a climatic gradient in western Canada. Weed Science 1092:1081-1092.

Strickland, M. S., C. Lauber, N. Fierer, and M. a Bradford. 2009. Testing the functional significance of microbial community composition. Ecology 90:441-451.

Stursova, M., and R. L. Sinsabaugh. 2008. Stabilization of oxidative enzymes in desert soil may limit organic matter accumulation. Soil Biology and Biochemistry 40:550-553.

Takacs-Vesbach, C., K. Mitchell, O. Jackson-Weaver, and A.-L. Reysenbach. 2008. Volcanic calderas delineate biogeographic provinces among Yellowstone thermophiles. Environmental Microbiology 10:1681-1689.

Takacs-Vesbach, C., L. Zeglin, J. E. Barrett, M. N. Gooseff, and J. C. Priscu. 2010. Factors promoting microbial diversity in the McMurdo Dry Valleys , Antarctica. pp. 221-257 *in* P. Doran, W. B. Lyons, and D. M. McKnight, eds. Life in Antarctic Deserts and Other Cold Dry Environments: Astrobiological Analogs. Cambridge University Press.

Tiedje, J. M., S. Asuming-Brempong, K. Nusslein, T. L. Marsh, and S. J. Flynn. 1999. Opening the black box of soil microbial diversity. Applied Soil Ecology 13:109-122.

Treonis, A. M., D. H. Wall, and R. A. Virginia. 1999. Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. Ecosystems 2:482-492.

Treonis, A. M., and D. H. Wall. 2005. Soil nematodes and desiccation survival in the extreme arid environment of the Antarctic Dry Valleys. Integrative and Comparative Biology 45:741-750.

Virginia, R. A., and D. H. Wall. 1999. How soils structure communities in the Antarctic Dry Valleys. BioScience 49:973-983.

Waldrop, M. P., T. C. Balser, and M. K. Firestone. 2001. Linking microbial community composition to function in a tropical soil. Soil Biology and Biochemistry 32:1837-1846.

Walker, T. W., and J. K. Syers. 1976. The fate of phosphorus during pedogenesis. Geoderma 15:1-19.

Whitaker, R. J., D. W. Grogan, and J. W. Taylor. 2003. Geographic barriers isolate endemic populations of hyperthermophilic archaea. Science 301:976-978.

Yannarell, A. C., and E. W. Triplett. 2005. Geographic and environmental sources of variation in lake bacterial community composition. Applied and Environmental Mcrobiology 71:227-239.

Zeglin, L. H., C. N. Dahm, J. E. Barrett, M. N. Gooseff, S. K. Fitpatrick, and C. D. Takacs-Vesbach. 2011. Bacterial community structure along moisture gradients in the parafluvial sediments of two ephemeral desert streams. Microbial Ecology 61:543-556.

Zeglin, L. H., R. L. Sinsabaugh, J. E. Barrett, M. N. Gooseff, and C. D. Takacs-Vesbach. 2009. Landscape distribution of microbial activity in the McMurdo Dry Valleys: Linked biotic processes, hydrology, and geochemistry in a cold desert ecosystem. Ecosystems 12:562-573.

Zhou, J., B. Xia, D. S. Treves, L. Wu, T. L. Marsh, R. V. O. Neill, A. V. Palumbo, and J. M. Tiedje. 2002. Spatial and resource factors influencing high microbial diversity in soil. Applied and Environmental Microbiology 68:326-334.