

# Landscape Distribution of Microbial Activity in the McMurdo Dry Valleys: Linked Biotic Processes, Hydrology, and Geochemistry in a Cold Desert Ecosystem

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## ABSTRACT

In desert ecosystems, microbial activity and associated nutrient cycles are driven primarily by water availability and secondarily by nutrient availability. This is especially apparent in the extremely low productivity cold deserts of the McMurdo Dry Valleys, Antarctica. In this region, sediments near streams and lakes provide the seasonally wet conditions necessary for microbial activity and nutrient cycling and thus transfer energy to higher organisms. However, aside from a few studies of soil respiration, rates of microbial activity throughout the region remain unexplored. We measured extracellular enzyme activity potentials (alkaline phosphatase, leucine-aminopeptidase, beta-glucosidase, phenol oxidase, and peroxidase) in soils adjacent to lakes and streams, expecting activity to be primarily related to soil water content, as well as

time of season and organic matter supply. Phosphatase and beta-glucosidase activities were higher in shoreline than upland soils; however, potential rates were not correlated with soil water content. Instead, soil organic matter, salinity, and pH were the best predictors of microbial activity. Microbial nutrient limitation metrics estimated from extracellular enzyme activity were correlated with pH and salinity and exhibited similar patterns to previously published trends in soil P and N content. Compared to other terrestrial ecosystems, organic matter specific rates for leucine-aminopeptidase and oxidative enzyme activities were high, typical of alkaline desert soils. Phosphatase activity was close to the global mean whereas beta-glucosidase activity was extremely low, which may reflect the lack of vascular plant derived organic matter in the Dry Valleys. In this cold desert ecosystem, water availability promotes microbial activity, and microbial nutrient cycling potentials are related to soil geochemistry.

**Key words:** desert; biogeochemistry; microbial ecology; extracellular enzyme activity; hydrologic margin; McMurdo Dry Valleys.

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## INTRODUCTION

The McMurdo Dry Valleys region of Antarctica is a polar desert characterized by extremely low annual precipitation (<100 mm) and an absence of vascular plants and vertebrates; microbial activity dominates biological functioning. Here, as in all deserts, biotic activity is constrained by temperature and substrate availability, but water is the primary limiting resource (Kennedy 1993; Noy-Meir 1973; Parsons and others 2004). Spatial and temporal heterogeneity in microbial activity and biogeochemical cycling in desert soils is linked to pulses of water availability and patches of organic matter (Aislabie and others 2006; Barrett and others 2008a; McKay and others 2003; Treonis and others 2000). Overall rates of microbial activity, measured as soil respiration, are directly related to the magnitude of available organic matter pools (Barrett and others 2006; Sponseller 2007). Regions of greater water and organic matter availability also harbor a greater diversity of soil organisms (Wall and Virginia 1999).

In the McMurdo Dry Valleys and other desert ecosystems, soils and sediments adjacent to waterbodies are the local hotspots of organic matter production and turnover (Austin and others 2004; Burkins and others 2001; Gregorich and others 2006; Treonis and others 1999). Because precipitation is both infrequent and low, seasonal water availability in hydrologically connected soils makes these aquatic–terrestrial transition zones more hospitable relative to dry upland soils. The hydrologic margin habitat has the most complex trophic structures in the region, as evidenced by high richness and abundance of invertebrates (Ayres and others 2007; Treonis and others 1999). Near shore microbial mats are the most apparent signs of life on the landscape, and mat production may supply a significant portion of the organic matter fueling life in the Dry Valleys (Fritsen and others 2000; Hopkins and others 2006; Moorhead and others 2003). Wetted soils are also important sites of chemical weathering (Gooseff and others 2002) and cycling of nitrogen (N) and phosphorus (P) (Barrett and others 2002; Bate and others 2008; McKnight and others 2004). Thus, microbial activity in these aquatic–terrestrial transition zones may affect the biogeochemistry of the entire dry valley ecosystem. Studies to date have focused on nutrient fluxes within and across the boundaries of these transition zones. Comparative studies of microbial community function along these gradients of moisture and nutrient availability can provide additional insight into the spatial and temporal dynamics of microbial activity in this landscape.

Estimation of extracellular enzyme activity (EEA) is a technique that directly assesses microbial activity and contribution to nutrient cycling (Sinsabaugh and others 2002). Extracellular enzymes are released by microbiota to degrade complex organic matter. Changes in decomposition rates and soil carbon (C) storage have been linked to shifts in the potential activity of the extracellular enzymes that degrade the major components of soil organic matter (Carreiro and others 2000; Sinsabaugh and others 2005; Waldrop and others 2004). Because microbes alter production of extracellular enzymes in response to environmental nutrient availability, ratios of activities directed toward C, N, and P acquisition can also be used as indicators of relative microbial nutrient limitation (Allison and others 2007; Sinsabaugh and others 2008). Other studies have shown that biological activity in streams and lakes of the McMurdo Dry Valleys is limited by N and P (Dore and Priscu 2001; McKnight and others 2004), but the geochemical constraints on soil microbial activity have not been studied.

We measured a suite of extracellular enzyme activities to investigate patterns of microbial activity throughout the McMurdo Dry Valleys (MCM). Because water availability is the primary control on biotic activity in this desert ecosystem (Kennedy 1993), we sampled soils from the wet margins and dry uplands adjacent to 11 lake and stream sites across three valleys. We expected to measure higher microbial activity, as EEA potentials, in the saturated soils near each waterbody. Samples were collected both early (early December) and late (mid January) in the 2005–2006 austral summer. Because the first flush of water following a long dry period can stimulate a pulse of microbial activity (Sponseller 2007), we predicted enzyme activity rates to be higher at the beginning of the season following activation by higher temperatures and advent of liquid water. Finally, though soil organic matter levels are extremely low in this cold desert, locally high concentrations can exist near waterbodies due to microbial mat production. Because higher rates of nutrient flux have been measured in soils with more organic matter (for example, Barrett and others 2006; Gregorich and others 2006), we expected greater EEA in areas with more organic matter content.

## METHODS

### Study Area and Sampling Sites

The McMurdo Dry Valleys, Victoria Land, Antarctica (MCM, 77°30'S 163°00'E) are among the most

extreme terrestrial environments. This 4800 km<sup>2</sup> area of ice-free polar desert receives less than 100 mm precipitation annually, most of which sublimates before accumulating on the surface. Mean summer high and winter low temperatures are  $-5$  and  $-30^{\circ}\text{C}$  (Doran and others 2002). Liquid water is present on average 8 weeks of the year, as glacial-melt streams, “moats” at the edges of permanently ice-covered meromictic lakes, and isolated ponds of collected permafrost melt in topographic depressions. There are no vascular plants present. Soils are primarily Anhyorthels and Anhyturbels: dry, low in nutrients and generally underlain by permafrost within a meter of the surface (Bockheim 1997). Dry Valley landscapes (lakes, streams, and soils) occur on glacial tills that vary in surface exposure ages over several orders of magnitude ( $\sim 10$ – $1000$  KY), which significantly influences local geochemistry and habitat suitability for resident biota (Bockheim 2002; Barrett and others 2007). More information on the long term studies of glacial, stream, lake, and soil components of this ecosystem is available from the McMurdo Dry Valleys Long Term Ecological Research program (<http://www.mcmlter.org>).

Soil samples were collected in December 2005 and January 2006 from the margins of lakes and streams at 11 sites throughout the region (within the Taylor, Wright, and Pearce Valleys, Figure 1). At each site, samples were collected at locations based upon their proximity to the waterbody to capture differences in microbial activity based on soil water content. These “near” and “far” samples

were collected along a transect perpendicular to the surface water edge, and located based upon the visible extent of the hydrologic margin at each site (Gooseff and others 2007): “near” samples were collected within the hydrologic margin at a point one-third of the distance between surface water boundary and visible wetted boundary ( $2.2 \pm 1.2$  m from surface water), whereas “far” samples were collected from a point 0.2 m beyond the visible wetted boundary ( $5.9 \pm 3.5$  m from surface water). These samples were collected within a larger network of replicated transects from which geochemical parameters were measured at a minimum of 16 points per site (Gooseff and others 2007, 2008; Northcott and others 2008). Samples were collected using a sterile scoop to a depth of 10 cm, and stored at  $-20^{\circ}\text{C}$  until analysis.

### Chemical Analyses

Each sediment sample was analyzed for KCl-extractable  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N, electrical conductivity (EC), pH, water content (WC), and organic matter (OM) content. Inorganic nitrogen was measured on 10 g soil extracted in 50 ml 2 M KCl.  $\text{NO}_3^-$ -N (as  $\text{NO}_2^-$ -N) and  $\text{NH}_4^+$ -N concentrations were measured colorimetrically using the sulfanilamide dihydrochloride and salicylate methods, respectively, on a Lachat Autoanalyzer. Soil temperature and conductivity were measured in the field using in situ probes. Soil pH was measured in a 1:1 ratio of soil and 10 mM  $\text{CaCl}_2$  solution. Water content and OM content were measured as soil

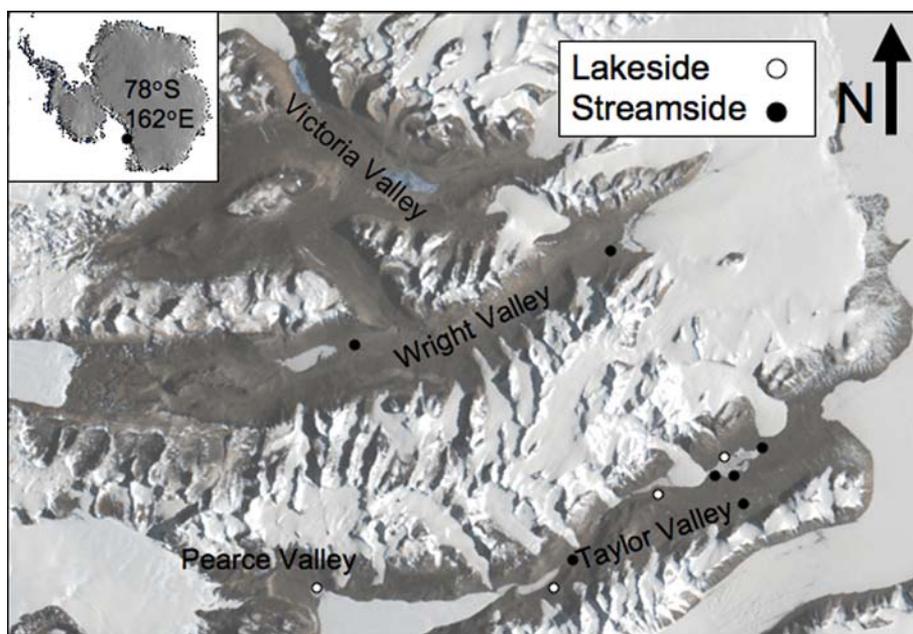


Figure 1. Map of the McMurdo Dry Valleys, Antarctica, including all eleven sampling sites.

mass loss upon drying at 100°C and combustion at 500°C, respectively. The potentially significant carbonate content of Dry Valleys soils may cause overestimation of soil OM with the loss on ignition (LOI) method, however, the SOM values reported here are comparable to known Dry Valleys soil values (Burkins and others 2000; Fritsen and others 2000; Hopkins and others 2006); also, using SOM from LOI allows direct comparison of soil EEA per unit SOM values to those measured in other ecosystems (Sinsabaugh and others 2008).

### Extracellular Enzyme Activity Assays

Each soil sample was assayed for the potential activities of three hydrolytic enzymes,  $\beta$ -glucosidase ( $\beta$ G; EC 3.2.1.21, using 4-methylumbelliferyl (MUB)- $\beta$ -D-glucoside), alkaline phosphatase (AP; EC 3.1.3.1, using 4-MUB-phosphate), and leucyl aminopeptidase (LAP; EC 3.4.11.1, using L-Leucine-7-amido-4-methylcoumarin), and two oxidative enzymes, phenol oxidase (POX; EC 1.10.3.2, using L-3,4-dihydroxyphenylalanine (DOPA)) and peroxidase (PER; EC 1.11.1.7, using DOPA and H<sub>2</sub>O<sub>2</sub>) following protocols previously presented (Saiya-Cork and others 2002; Stursova and others 2006; Zeglin and others 2007).

Our protocol varied from these previously published microplate protocols in that all assays were conducted using larger volumes and greater ratios of soil:substrate because of the low OM content of the samples. For each assay, 0.5 g soil, 0.7 ml of 50 mM bicarbonate buffer, and 0.7 ml of substrate solution (200  $\mu$ M for hydrolases, 5 mM for oxidases) were added to a 1.5 ml microcentrifuge tube, which was capped and vortexed. For the BG, AP, and LAP assays, the final substrate concentration was 100  $\mu$ M. For POX and PER assays, the final DOPA concentration was 2.5 mM (plus 4.4 mM H<sub>2</sub>O<sub>2</sub> for PER). The fluorimetric assays included negative controls that measure background fluorescence of substrates and samples, and positive controls that compare the fluorescence of a 10  $\mu$ M MUB standard in both buffer and sample + buffer mixtures. The colorimetric assays included negative controls for sample and substrate absorbance. Assays were conducted in triplicate, at pH 8.2 to approximate ambient soil pH and incubated at 20°C, to optimize psychrophilic enzyme activity and permit comparisons to EEA potentials measured in other systems. To facilitate comparisons across ecosystems, enzyme activities were normalized for sample organic matter content. BG, AP, and LAP activities are reported as nmol h<sup>-1</sup> g<sup>-1</sup> OM; POX and PER activities are reported as

$\mu$ mol h<sup>-1</sup> g<sup>-1</sup> OM. Due to limited quantities of sample, oxidative enzyme activities were assayed only on a subset ( $n = 10$ ) of the 44 samples collected.

To evaluate relative nutrient limitation of microbial communities in these sediments, ratios of BG:LAP, BG:AP, and LAP:AP activity were compared as indicators of C:N, C:P, and N:P acquisition investment tradeoffs. These ratios were analyzed as another subset of dependent variables within the full dataset.

### Microbial Biomass and DOC

Microbial biomass C (MBC) was measured as the difference in soil K<sub>2</sub>SO<sub>4</sub>-extractable DOC between chloroform fumigated and unfumigated subsamples (Scott-Denton and others 2005). Three replicates of 5 g subsamples of soil from each collection point were fumigated for 24 h with 2 ml ethanol-free chloroform, fully air dried (2–3 h) in a fume hood, and then were extracted with 0.5 M K<sub>2</sub>SO<sub>4</sub> for 30 min. DOC from unfumigated soil subsamples was concurrently extracted. DOC concentration of filtered K<sub>2</sub>SO<sub>4</sub> extracts was measured using a UV-persulfate TOC analyzer. The unfumigated K<sub>2</sub>SO<sub>4</sub>-extractable DOC value was also used to represent the soil available DOC concentration.

### Statistical Analyses

Multivariate analysis of variance (MANOVA) was used to compare edaphic characteristics and enzyme activities of soil samples in relation to sampling location (near and far) and sampling date (early and late season). Four MANOVA analyses were run with different sets of dependent variables: edaphic metrics, hydrolytic enzyme activities, oxidative enzyme activities, and hydrolytic enzyme activity ratios. To evaluate differences in microbial activity between near/far and early/late collections at each site and between other categories of spatial distribution (that is, between valleys and surface water types (stream versus lake)), data were analyzed using one-way analysis of variance (ANOVA), and post-hoc multiple comparisons were made using the Bonferroni method.

The strength and significance of correlations between microbial activity and edaphic characteristics are reported using Pearson's  $r$  and two-tailed significance values. Multiple linear regressions to predict hydrolytic EEA from edaphic variables (water content, OM content, extractable DIN, extractable DOC, temperature, conductivity, pH, etc.) were conducted using forward stepwise variable addition and model evaluation. Soil physical

and chemical data were distributed normally and EEA data were normalized by natural log transformation before performing statistical analyses. SPSS 11 for Mac (Chicago, IL) was used for all statistical analyses.

## RESULTS

Environmental data collected from soils above and below the hydrologic margins of surface waters fall within the ranges reported for soils in previous landscape level studies of the McMurdo Dry Valleys for temperature (Barrett and others 2008b; Doran and others 2002; Gooseff and others 2008), conductivity, pH, nutrient, and organic matter concentrations (for example, Barrett and others 2007; Fritsen and others 2000), and are typical of other poorly developed desert soils in terms of pH, and nutrient and organic matter concentrations (Stursova and others 2006). Soils and sediments in hydrological margins of the McMurdo Dry Valleys had high pH ( $\sim 8.6$ ) and very low concentrations of soil organic matter (SOM,  $\sim 0.5\%$ ) and inorganic N ( $\sim 0.0006\%$ ) (Table 1).

MANOVA of edaphic variables by sampling date and proximity to the surface water boundary showed no difference for any soil chemistry variable by date (early versus late summer), and only one significant date by proximity interaction for extractable DOC ( $P = 0.022$ ). Water content was

the only variable that varied with proximity to the surface water (16.2% by mass in "near" soils and 3.2% in "far" soils,  $P < 0.001$ ). Other comparisons showed that electrical conductivity was greater within the hydrologic margins of lakes compared to streams ( $413 \mu\text{S} > 5.6 \mu\text{S}$ ,  $P = 0.002$ ).

Temperature, electrical conductivity, and pH also differed significantly among lake basins, based on one-way ANOVA results (Table 2). Vanda basin (Wright Valley) soils had the lowest temperature and pH, whereas Fryxell basin (Taylor Valley) soils were the warmest and had the highest pH. Bonney basin (Taylor Valley) soils had the highest conductivity (an index of salinity), exceeding the other basins by at least one order of magnitude. Although temperatures reported here represent surface soil conditions at the time points of collection only, the basin scale differences in temperature are consistent with other measurements made at greater spatial and temporal resolution for the same sites (Ikard and others 2009; Northcott and others 2008) and with patterns documented by others over greater time periods (Doran and others 2002). The same is true for geochemical measurements: the basin scale differences are consistent with other concurrently collected data (Barrett and others in press) and previously documented distributions of soil C, N, and P (Fritsen and others 2000; Barrett and others 2007). Differences in pH among basins may be related to the relative soil age in each val-

**Table 1.** Means ( $\pm$ SE) of Edaphic, Biogeochemical and Microbial Activity (EEA) Metrics for Soils Collected from Points Within (near) and Above (far) the Hydrologic Margin of Waterbodies at 11 Sites throughout the McMurdo Dry Valleys

	Near Mean ( $\pm$ SE)	Far Mean ( $\pm$ SE)
Distance from surface water (m)	2.16 <sup>a</sup> ( $\pm 0.25$ )	5.93 <sup>b</sup> ( $\pm 0.76$ )
pH	8.54 ( $\pm 0.13$ )	8.76 ( $\pm 0.13$ )
Temperature ( $^{\circ}\text{C}$ )	5.1 ( $\pm 0.54$ )	5.4 ( $\pm 0.61$ )
EC ( $\mu\text{S}$ )	134 ( $\pm 8.4$ )	142 ( $\pm 9.8$ )
Water content ( $\text{g g}^{-1}$ dry soil)	0.162 <sup>a</sup> ( $\pm 0.012$ )	0.032 <sup>b</sup> ( $\pm 0.007$ )
$\text{NO}_3\text{-N}$ ( $\mu\text{g g}^{-1}$ dry soil)	3.2 ( $\pm 1.5$ )	7.1 ( $\pm 3.5$ )
$\text{NH}_4\text{-N}$ ( $\mu\text{g g}^{-1}$ dry soil)	1.2 ( $\pm 0.68$ )	0.24 ( $\pm 0.08$ )
TIN ( $\mu\text{g g}^{-1}$ dry soil)	4.4 ( $\pm 1.6$ )	7.3 ( $\pm 3.5$ )
OM content ( $\text{mg g}^{-1}$ dry soil)	4.9 ( $\pm 0.7$ )	5.9 ( $\pm 1.0$ )
Extractable DOC ( $\mu\text{g g}^{-1}$ dry soil)	18.2 ( $\pm 4.4$ )	28.5 ( $\pm 8.5$ )
Microbial biomass C ( $\mu\text{g g}^{-1}$ dry soil)	62.0 ( $\pm 30.5$ )	15.0 ( $\pm 4.6$ )
$\beta$ -Glucosidase ( $\text{nmol h}^{-1} \text{g}^{-1}$ OM)	115 <sup>a</sup> ( $\pm 19$ )	111 <sup>b</sup> ( $\pm 23$ )
Leucyl aminopeptidase ( $\text{nmol h}^{-1} \text{g}^{-1}$ OM)	3528 ( $\pm 378$ )	4138 ( $\pm 486$ )
Phosphatase ( $\text{nmol h}^{-1} \text{g}^{-1}$ OM)	3612 <sup>a</sup> ( $\pm 438$ )	2562 <sup>b</sup> ( $\pm 325$ )
Phenol oxidase ( $\mu\text{mol h}^{-1} \text{g}^{-1}$ OM)	573 ( $\pm 176$ )	189 ( $\pm 90$ )
Peroxidase ( $\mu\text{mol h}^{-1} \text{g}^{-1}$ OM)	264 ( $\pm 192$ )	129 ( $\pm 85$ )

Significant differences (ANOVA,  $P < 0.05$ ) between near and far soils are denoted by superscripts.

**Table 2.** Mean Edaphic and EEA Values ( $\pm$ SE) by Lake Basin with Additional Information on Soil Age and Nutrient Stoichiometry

	Fryxell	Hoare	Bonney	Joyce	Vanda
Soil age (KY) <sup>1</sup>	8–24	75–98	75–98	200–2000	10.3–1000
C:N <sup>2</sup>	25.1	7.00	6.41	1.07	na
N:P <sup>2</sup>	0.06	0.28	0.28	1.20	na
Temp (°C)	6.84 <sup>a</sup> ( $\pm$ 0.45)	3.16 <sup>ab</sup> ( $\pm$ 1.5)	5.19 <sup>ab</sup> ( $\pm$ 0.64)	3.83 <sup>ab</sup> ( $\pm$ 0.83)	2.76 <sup>b</sup> ( $\pm$ 0.72)
EC ( $\mu$ S)	26.8 <sup>ab</sup> ( $\pm$ 13)	bdl	657 <sup>b</sup> ( $\pm$ 275)	2.5 <sup>a</sup> ( $\pm$ 2.5)	bdl
pH	8.9 <sup>a</sup> ( $\pm$ 0.1)	8.6 <sup>ab</sup> ( $\pm$ 0.2)	8.6 <sup>ab</sup> ( $\pm$ 0.1)	8.7 <sup>ab</sup> ( $\pm$ 0.2)	8.0 <sup>b</sup> ( $\pm$ 0.3)
OM (mg g <sup>-1</sup> )	7.0 ( $\pm$ 0.9)	4.0 ( $\pm$ 1.3)	5.6 ( $\pm$ 1.4)	4.0 ( $\pm$ 1.0)	2.3 ( $\pm$ 0.6)
$\beta$ G	145 <sup>a</sup> ( $\pm$ 19)	40.3 <sup>b</sup> ( $\pm$ 15)	165 <sup>ab</sup> ( $\pm$ 59)	29.8 <sup>b</sup> ( $\pm$ 16)	39.5 <sup>b</sup> ( $\pm$ 7.9)
LAP	4610 <sup>a</sup> ( $\pm$ 496)	5235 <sup>a</sup> ( $\pm$ 572)	2735 <sup>b</sup> ( $\pm$ 646)	1045 <sup>b</sup> ( $\pm$ 201)	3043 <sup>ab</sup> ( $\pm$ 606)
AP	2746 <sup>ab</sup> ( $\pm$ 379)	4195 <sup>b</sup> ( $\pm$ 347)	2187 <sup>a</sup> ( $\pm$ 474)	1339 <sup>a</sup> ( $\pm$ 296)	4570 <sup>b</sup> ( $\pm$ 857)

Metrics include temperature (Temp), electrical conductivity (EC, a proxy for salinity), soil organic matter content (OM), beta-glucosidase activity ( $\beta$ G, nmol h<sup>-1</sup> g<sup>-1</sup> OM), L-aminopeptidase activity (LAP, nmol h<sup>-1</sup> g<sup>-1</sup> OM), and alkaline phosphatase activity (AP, nmol h<sup>-1</sup> g<sup>-1</sup> OM). ANOVA post-hoc groupings of differences in each variable ( $P < 0.05$ ) between basins are denoted by superscripts.

<sup>1</sup>Barrett and others (2007); Bate and others (2008); Bockheim (2002).

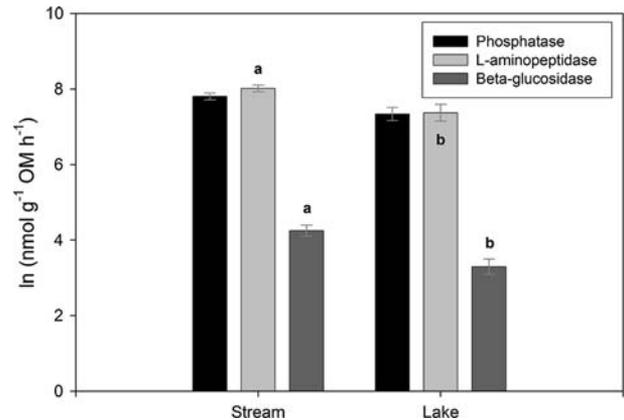
<sup>2</sup>Barrett and others (2007).

ley. Older soils are more depleted in P and have lower pH due to more extensive weathering, and are also more enriched in N and C due to accumulation of solutes and organic matter over time (Barrett and others 2007; Bate and others 2008).

MANOVA of hydrolytic enzyme activities (BG, AP, and LAP) showed no significant sampling date or date by surface water proximity interaction effects. However, BG and AP activities were significantly greater for soils in the wetted hydrologic margin compared to the upland samples ( $P = 0.027$  and 0.037, respectively, Table 1).

Spatial differences in site responses were apparent between aquatic system types (stream versus lake) and among lake basins. BG and LAP activities were higher in stream margin soil than lake margin soil (Figure 2,  $P = 0.044$  and 0.043, respectively). Hydrolytic enzyme activities also differed by lake basin (Table 2), with the Joyce basin (Pearse Valley) having the lowest and the Hoare basin (Taylor Valley) the highest organic matter specific activity rates.

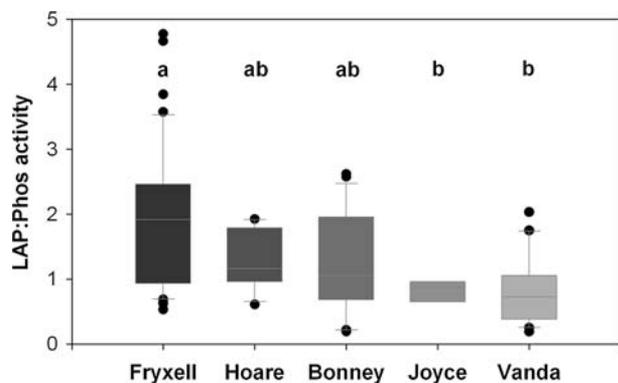
Within sites, ANOVA showed significant variations in hydrolytic EEA in relation to moisture and sampling date at all sites. These post hoc site-by-site results fit our spatial and temporal predictions that EEA was greater in soils within the hydrologic margin compared to upland samples in only 22 of 50 comparisons and activities were greater in early summer compared to late summer for only 18 of 47 comparisons. The remainder of comparisons either showed no significant difference or did not fit our predictions. Because spatial and temporal patterns varied among sites, there was no significant sea-



**Figure 2.** Hydrolytic enzyme activities in lakes and stream edge sediments of the McMurdo Dry Valleys. The means ( $\pm$ SE) of ln beta-glucosidase activity (BG), L-aminopeptidase activity (LAP) and alkaline phosphatase activity (AP) in stream and lake margin soils are shown. Lower case letters denote an ANOVA-significant difference ( $P < 0.05$ ) between the waterbody type in the potential activity of an extracellular enzyme.

sonal effect for the regional dataset within the MANOVA comparisons.

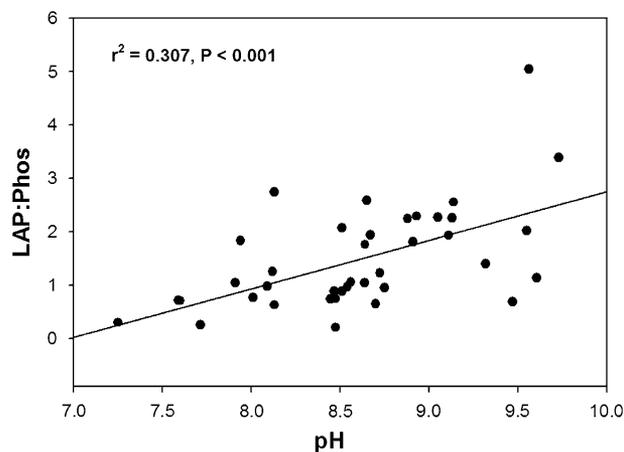
The MANOVA results for oxidative activities (peroxidase and phenol oxidase) showed no statistically significant spatial (near/far), temporal (early/late season), or interaction effects. However, peroxidase activities were generally greater in near shore soils compared to upland soils ( $P = 0.059$ ) and phenol oxidase activities trended toward higher values in early season samples compared to late season samples ( $P = 0.063$ ).



**Figure 3.** Nutrient limitation of microbial activity varies among basins of the McMurdo Dry Valleys. ANOVA post-hoc groupings (Bonferonni method) of significant differences ( $P < 0.05$ ) between basins are denoted by lower case letters. Box boundaries represent upper and lower 50% confidence intervals, bars represent upper and lower 95% confidence intervals and dots represent outliers with values outside of upper and lower 95% confidence intervals.

Enzyme activity ratios (BG:LAP, BG:AP, and LAP:AP) were not affected by time of season or the interaction between location and season. However, BG:LAP was greater in shoreline soils than in upland soils ( $P = 0.043$ ) and LAP:AP was greater in upland soils compared to shoreline soils ( $P = 0.028$ ). There was high site-by-site variability in microbial nutrient acquisition tradeoff, as there was for the component EEA values themselves, with a significant basin effect (ANOVA,  $P < 0.05$ ). LAP:AP was highest in the Fryxell basin and lowest in the Joyce and Vanda basins (Figure 3, Table 2). For the entire dataset, BG:LAP ratio correlated only with EC ( $r = 0.49$ ,  $P = 0.001$ ), BG:AP correlated only with OM ( $r = 0.37$ ,  $P = 0.015$ ), and LAP:AP correlated only with pH (Figure 4,  $r = 0.56$ ,  $P < 0.001$ ).

Finally, because our original expectation that soil water content would drive microbial activity was not confirmed, we ran multiple linear regressions on the full dataset to learn which edaphic variables were useful in predicting hydrolytic EEA in McMurdo Dry Valleys soils. No model could predict BG activity with any reliability. The best model for predicting LAP activity ( $r^2 = 0.564$ ,  $P < 0.001$ ) included EC ( $t = -4.982$ ,  $P < 0.001$ ), pH ( $t = 3.552$ ,  $P = 0.001$ ), and OM ( $t = -3.227$ ,  $P = 0.003$ ). The best model of AP activity ( $r^2 = 0.531$ ,  $P < 0.001$ ) included OM ( $t = -5.008$ ,  $P < 0.001$ ) and EC ( $t = -3.838$ ,  $P = 0.001$ ). For these two models, the relationship between OM and activity was negative, and soil water content was not an important factor in either.



**Figure 4.** L-aminopeptidase to phosphatase ratio as a function of soil pH in hydrologic margins of streams and lakes in the McMurdo Dry Valleys, Antarctica.

## DISCUSSION

### Distribution of Enzyme Activity in McMurdo Dry Valleys Soils

We hypothesized that proximity to surface water and time of season would affect EEA potential in McMurdo Dry Valley soils by promoting microbial growth and accumulation of organic matter.  $\beta$ -glucosidase and phosphatase activities were higher (3.6% and 41% higher, respectively) in the hydrologic margins compared to upland soils, but time of season did not affect EEA. Enzyme activities were higher in moist near-stream margins than dry soils, although soil water content at the time of sampling did not directly correlate with the potential activity of any extracellular enzyme. Microbial activity in soils with higher connectivity to a waterbody may be promoted by higher rates of nutrient flux. In concordance with this idea,  $\beta$ -glucosidase and leucine-aminopeptidase activities were greater in stream margin soils, where flowing water delivers a higher amount of material over time, than lake margin soils.

Multiple linear regressions showed that sediment conductivity and organic matter content (and pH for leucine-aminopeptidase) were the geochemical factors that best predicted phosphatase and leucine-aminopeptidase potential. It is somewhat surprising that temperature is not a significant factor in predicting microbial activity. Although our temperature data are consistent with previously published valley scale trends (Wright Valley is cooler than Taylor Valley), surface soil temperature varies daily and even hourly based on changes in solar radiation (Gooseff and others 2008; Ikard and others

2009). Therefore, our point measurements of temperature may not be representative of the seasonal changes in temperature expected to affect microbial activity (Treonis and others 2002; Yergeau and Kowalchuk 2008) as measured by soil extracellular enzyme potentials.

The importance of organic matter as a substrate for EEA is inherent to soil food web energetics. However, the negative relationship between organic matter specific activity and organic matter concentration is not typical: at global scales hydrolytic EEA per gram soil is closely related to SOM such that specific activity tends to remain relatively constant (Sinsabaugh and others 2008). However, in these low organic matter soils, the stabilization of enzymes on mineral surfaces may overwhelm this trend (Stursova and Sinsabaugh 2008). In addition, higher soil organic matter content within the Dry Valley ecosystems is associated with a higher proportion of potentially refractory carbon derived from lake sediments (Burkins and others 2000): smaller pools of more labile organic matter may support higher levels of microbial activity (Barrett and others 2006).

Salinity has been shown to control the distributions of invertebrate taxa throughout the Dry Valleys (Poage and others 2008; Treonis and others 1999). Salinity exerts osmotic stress on biota, which for microorganisms could result in lower production of extracellular enzymes. Alternatively, high salinity can reduce the capacity of soils to immobilize extracellular enzymes, which may also contribute to lower potential EEA.

LAP activity was positively correlated with soil pH, whereas AP activity and pH exhibited no relationship. Aminopeptidases are generally most efficient at high pH, whereas phosphatases can be either acid or alkaline, which makes it likely that

potential activity will show less variation in relation to soil pH (Sinsabaugh and others 2008). The strong relationship between conductivity, pH, and EEA values suggests that edaphic variables may be important in physiologically constraining microbial function.

Basin scale differences in EEA values and EEA ratios may reflect differences in substrate availability and soil properties. Mean EEA values should be proportional to overall microbial activity, and EEA ratios should vary based on the relative investment of microbes toward acquisition of limiting nutrients. Although  $\beta$ G ratios may not be the optimal measurement of total carbon acquisition in an environment devoid of vascular vegetation, patterns of leucine-aminopeptidase to phosphatase activity ratios are quite interesting. LAP:AP varied by an order of magnitude (0.4–4.0), and decreased from the youngest to oldest lake basins (Table 3, Figure 3), indicating that relatively more energy is invested in acquiring phosphate from organic matter in older soils. Soil pH may also be a factor. The younger soils (for example, Fryxell Basin) have higher pH than older soils (for example, Joyce Basin; Table 2), and soil pH is positively correlated with LAP activity (Figure 4). This observation makes sense, as pH is a primary control of EEA at the biochemical level: peptidase enzymes operate more efficiently at basic pH. It is interesting to note that soil biodiversity, like EEA, also varies at the basin scale (Ayres and others 2007; Barrett and others 2004).

### Comparison with Microbial Activity in Other Dry Valleys Habitats and Temperate Ecosystems

EEA has been measured in other habitats within the McMurdo Dry Valleys. Phosphatase activity

**Table 3.** Reported Values of Soil EEA for Different Biomes, Including This Study

	$\beta$ G	LAP	Perox	$\beta$ G:LAP	$\beta$ G:Perox	pH	Reference
McMurdo Dry Valleys	119	3916	420000	0.03	0.00028	8.7	This study
SEV (NM)	1842	6306	1837000	0.29	0.0010	7.6	Zeglin and others (2007)
KNZ (KS)	3008	200	831	15.0	3.62	5.5	Zeglin and others (2007)
Ukulunga (South Africa)	2612	45	2077	58.0	1.26	4.8	Zeglin and others (2007)
Manistee (MI) SMBW	4920	396	25000	12.4	0.197	5.5	Sinsabaugh and others (2005)
Manistee (MI) ROWO	2220	131	83500	16.9	0.027	5.5	Sinsabaugh and others (2005)
Niwot Ridge (CO)	2260	39	1480	57.9	1.53	5.5	M. Weintraub, pers. comm.
Duke FACE (NC)	4570	96	80900	47.6	0.057	5.5	Finzi and others (2006)
ORNL FACE (TN)	13500	561	124000	24.1	0.011	5.5	Sinsabaugh and others (2003)

McMurdo and Sevilleta (SEV), the two desert sites, stand apart from the rest in both EEA and pH. Table modified from Stursova and others (2006). Variables shown include beta-glucosidase activity ( $\beta$ G,  $\text{nmol h}^{-1} \text{g}^{-1}$  OM), L-aminopeptidase activity (LAP,  $\text{nmol h}^{-1} \text{g}^{-1}$  OM) and peroxidase activity (Perox,  $\text{nmol h}^{-1} \text{g}^{-1}$  OM). Other abbreviations include: New Mexico USA (NM), Kansas USA (KS), Michigan USA (MI), sugar maple/black walnut forest (SMBW), red oak/white oak forest (ROWO), Colorado USA (CO), Free Air Carbon Enrichment experiment (FACE), North Carolina USA (NC), Oak Ridge National Laboratory (ORNL), Tennessee USA (TN).

under saturating conditions in Lake Bonney is approximately  $13500 \text{ nmol g}^{-1} \text{ TOC h}^{-1}$  (Dore and Priscu 2001) compared to an average value of  $8000 \text{ nmol g}^{-1} \text{ TOC h}^{-1}$  (assuming OM is 45% carbon) for soils near the hydrological margins of lakes and streams. This suggests that lake microbiota are either investing more resources to acquire P than soil microbiota or that microbial activity in general is greater in the lake water column than in soils; both of these explanations are likely given the extreme paucity of P availability in lakes (Dore and Priscu 2001) and the overall low rates of biological activity in soils (Parsons and others 2004). The second explanation is consistent with the fact that overall nutrient availability and environmental stability is greater in the amictic lake water columns than the stream channel soils. Additionally, N:P ratios in Lake Bonney surface water are more imbalanced than soils (400:1 or higher vs. 4:1 or less, Barrett and others 2007), so lake microbiota may also display higher phosphatase activity due to greater P limitation. However, without corresponding measurements of microbial EEA investment in the acquisition of other nutrients from the lake water column, direct comparison between the two habitats is not possible.

BG, LAP, and AP potentials measured for cryoconite ice and sediment on alpine glaciers feeding Dry Valleys streams (Foreman and others 2007) ranged from 0.4 to 1.0,  $<0.1$  to 10, and 0.2 to  $2.0 \text{ nmol h}^{-1} \text{ g}^{-1} \text{ DOC}$ , respectively, with LAP:BG ratios of 1.2–37.4 and LAP:AP ratios of approximately less than 1–9. These activities are lower than those measured in the soils along the hydrologic margin, but the EEA ratios are similar (mean soil LAP:BG and LAP:AP ratios were 28.2 and 1.4, respectively). Maximum potential activity ( $V_{\text{max}}$ ) levels of endolithic phosphatase activity ranged from approximately  $50$  to  $500 \text{ nmol g}^{-1} \text{ rock matrix h}^{-1}$ , about 10 times greater than the  $1.1$ – $27 \text{ nmol g}^{-1} \text{ dry soil h}^{-1}$  measured in hydrologically-connected soils (Banerjee and others 2000).

In comparison to rates in other ecosystems, EEA potentials in the Dry Valleys soils were low on a mass specific basis (per gram soil, mostly ranging from  $10^1$  to  $10^2 \text{ nmol h}^{-1}$ ) but generally comparable to other ecosystems when compared on an organic matter specific basis. Rates of specific LAP activity in the McMurdo Dry Valleys were typical of alkaline soils in desert ecosystems, where potentials may be 2–3 orders of magnitude greater than those of acidic soils of mesic ecosystems (Sinsabaugh and others 2008; Zeglin and others 2007). Phosphatase

activity in McMurdo Dry Valleys soils is close to the global mean of  $5300 \text{ nmol h}^{-1} \text{ g}^{-1} \text{ SOM}$  (Sinsabaugh and others 2008).

The relatively high specific enzyme activity measured in this study may be in part related to the prevalence of psychrophilic organisms in the Dry Valleys environment. Psychrophilic and psychrotolerant bacteria may use one of two strategies to operate at low temperatures: produce enzymes that operate optimally at lower temperatures, or increase production of enzymes to compensate for lower rates of catalysis, which enables a high pulse of activity when temperatures rise (Feller and Gerday 1997).

Beta-glucosidase is the exception: activity per gram OM ( $\sim 110 \text{ nmol}^{-1} \text{ h}^{-1} \text{ g}^{-1} \text{ OM}$ ) in the McMurdo Dry Valleys is lower than values reported for any other ecosystem (Table 3). On a global basis mean BG activity is  $3320 \text{ nmol h}^{-1} \text{ g}^{-1} \text{ SOM}$  (Sinsabaugh and others 2008). Beta-glucosidase activity was also unusual in that it could not be predicted by multiple linear regression models based on soil biogeochemical parameters, suggesting that the variability in this metric is insensitive to the environmental variables measured in this study. These anomalous values, particularly when juxtaposed with specific LAP and AP activities that are typical for desert ecosystems, probably reflect the absence of vascular plants, and therefore cellulose as a major component of SOM. Although residuals of ancient or distant-sourced vascular plant matter are present in MCM soil organic matter (Matsumoto and others 1990), modern vascular plant detrital contribution to sediment OM is negligible.

The lack of vascular plant inputs to SOM in the Dry Valleys suggests that phenol oxidase and peroxidase activities should also be depressed compared to other ecosystems. Fulvic acids are present in stream and lake moat waters, but in much lower proportions (6–13%) than other freshwaters (Aiken and others 1996). However, peroxidase and phenol oxidase activities, like those of LAP, were typical of alkaline desert soils, where potentials exceed those of wetter ecosystems by 2–3 orders of magnitude. Recent studies in other desert ecosystems have shown that these enzymes may be stabilized by association with mineral surfaces (Stursova and Sinsabaugh 2008), and hence are not always indicative of contemporary biological activity.

Overall, the distribution of both hydrolytic and oxidative enzyme activities, with the exception of BG, was similar to those reported for other eco-

systems, particularly arid ecosystems (Sinsabaugh and others 2008). Despite strong differences in organic matter composition between the McMurdo Dry Valleys and temperate deserts, edaphic characteristics common to all arid soils (in particular, high pH and conductivity) may maintain biochemical controls on microbial function. Other studies have shown soil EEA potentials both within and between ecosystems to be strongly related to soil pH (Sinsabaugh and others 2008; Zeglin and others 2007). The patterns of inter-basin differentiation of microbial function and the correlation between EEA rates and basic edaphic characteristics in the McMurdo Dry Valleys reflect the distribution of biogeochemical activity across the region (Barrett and others 2006) as well as other arid (Stursova and others 2006) and temperate (Sinsabaugh and others 2008) soils. Although water availability promotes higher microbial activity in the cold desert of the McMurdo Dry Valleys, potential rates of microbially-mediated nutrient turnover are also related to soil pH, organic matter availability, and salinity.

Edaphic characteristics related to soil age and weathering status constrain biogeochemical cycling and macrobiotic distribution across the McMurdo Dry Valleys (Barrett and others 2007; Poage and others 2008). Extracellular enzyme activities vary among lake basins in a manner compatible with descriptions of soil age related distributions of C, N, P, and pH, suggesting that soil microbial activity could be constrained by geochemical factors as well as hydrological factors. The distribution of microbial activity in hydrologically active soils across the polar desert of the McMurdo Dry Valleys both reflects the unique organic matter composition of the ecosystem and suggests that microbial activity is related to similar soil characteristics as in temperate deserts and other temperate terrestrial ecosystems.

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