Primary productivity as a control over soil microbial diversity along environmental gradients in a polar desert ecosystem

Kevin M. Geyer Corresponding Author, Cristina D. Takacs-Vesbach, Michael N. Gooseff, John E. Barrett

1 Department of Natural Resources & the Environment, University of New Hampshire, Durham, NH, United States
2 Department of Biology, University of New Mexico, Albuquerque, NM, United States
3 Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO, United States
4 Department of Civil, Environmental & Architectural Engineering, University of Colorado, Boulder, CO, United States
5 Department of Biological Sciences, Virginia Tech, Blacksburg, VA, United States

Corresponding Author: Kevin M. Geyer
Email address: kevin.geyer@unh.edu

Primary production is the fundamental source of energy to foodwebs and ecosystems, and is thus an important constraint on soil communities. This coupling is particularly evident in polar terrestrial ecosystems where biological diversity and activity is tightly constrained by edaphic gradients of productivity (e.g., soil moisture, organic carbon availability) and geochemical severity (e.g. pH, electrical conductivity). In the McMurdo Dry Valleys of Antarctica, environmental gradients determine numerous properties of soil communities and yet relatively few estimates of gross or net primary productivity (GPP, NPP) exist for this region. Here we describe a survey utilizing pulse amplitude modulation (PAM) fluorometry to estimate rates of GPP across a broad environmental gradient along with belowground microbial diversity and decomposition. PAM estimates of GPP ranged from an average of 0.27 µmol O₂/m²/s in the most arid soils to an average of 6.97 µmol O₂/m²/s in the most productive soils, the latter equivalent to 217 g C/m²/y in annual net primary production assuming a 60 day growing season. A diversity index of four carbon-acquiring enzyme activities also increased with soil productivity, suggesting that the diversity of organic substrates in mesic environments may be an additional driver of microbial diversity. Overall, soil productivity was a stronger predictor of microbial diversity and enzymatic activity than any estimate of geochemical severity. These results highlight the fundamental role of environmental gradients to control community diversity and the dynamics of ecosystem-scale carbon pools in arid systems.
Primary productivity as a control over soil microbial diversity along environmental gradients in a polar desert ecosystem

Kevin M. Geyer¹, Cristina D. Takacs-Vesbach², Michael N. Gooseff³,⁴ and J. E. Barrett⁵

¹ Department of Natural Resources & the Environment, University of New Hampshire, Durham, New Hampshire USA
² Department of Biology, University of New Mexico, Albuquerque, New Mexico USA
³ Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado USA
⁴ Department of Civil, Environmental & Architectural Engineering, University of Colorado, Boulder, Colorado USA
⁵ Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia USA

† Email: kevin.geyer@unh.edu

Abstract

Primary production is the fundamental source of energy to foodwebs and ecosystems, and is thus an important constraint on soil communities. This coupling is particularly evident in polar terrestrial ecosystems where biological diversity and activity is tightly constrained by edaphic gradients of productivity (e.g., soil moisture, organic carbon availability) and geochemical severity (e.g. pH, electrical conductivity). In the McMurdo Dry Valleys of Antarctica, environmental gradients determine numerous properties of soil communities and yet relatively few estimates of gross or net primary productivity (GPP, NPP) exist for this region. Here we describe a survey utilizing pulse amplitude modulation (PAM) fluorometry to estimate rates of GPP across a broad environmental gradient along with belowground microbial diversity and decomposition. PAM estimates of GPP ranged from an average of 0.27 µmol O₂/m²/s in the most arid soils to an average of 6.97 µmol O₂/m²/s in the most productive soils, the latter equivalent to 217 g C/m²/y in annual net primary production assuming a 60 day growing season. A diversity index of four carbon-acquiring enzyme activities also increased with soil productivity, suggesting that the diversity of organic substrates in mesic environments may be an additional driver of microbial diversity. Overall, soil productivity was a stronger predictor of microbial diversity and enzymatic activity than any estimate of geochemical severity. These results highlight the fundamental role of environmental gradients to control community diversity and the dynamics of ecosystem-scale carbon pools in arid systems.
Primary production plays a fundamental role in controlling terrestrial foodwebs by making available the resources that regulate consumer productivity (Lindeman 1942; Tilman 1982; McNaughton et al. 1989) and shape community diversity (Waide et al. 1999; Judd et al. 2006). Rates of primary production also reflect the geochemical suitability of habitats for soil organisms (Chapin 1980), and thus much valuable information about the abiotic and biotic components of soil ecosystems can be inferred through knowledge of carbon fixation rates. Arid soils like those of the McMurdo Dry Valleys of Antarctica exemplify the tight coupling between ecosystem process rates and soil biological/geochemical properties. Here the landscape is dominated by alkaline (pH > 9.0), saline (conductivity >500 μS/cm), dry (gravimetric moisture < 1%) and low organic matter (< 0.03% organic C by weight) soils (Barrett et al. 2004) that support a very limited diversity of microfauna and no vascular plant or vertebrates species (Adams et al. 2006). However, seasonal wetting of stream and lake margins in this polar desert ameliorates the environmental severity and fosters dense cryptogamic mats of cyanobacteria and moss (Barrett et al. 2009). Such primary production reinforces the habitability of these hotspots for diverse microbial organotrophs through amendments of organic carbon (Treonis et al. 1999; Simmons et al. 2009; Geyer et al. 2013).

Despite a long history of researching environmental controls over Dry Valley soil diversity (Virginia and Wall 1999; Barrett et al. 2006b; Cary et al. 2010; Lee et al. 2012), efforts to measure rates of terrestrial gross or net primary production (GPP, NPP) in this system have been few. Rates of carbon fixation are near the levels of instrumental detection for gas exchange techniques and the growth rate of cryptogams does not lend itself to growth-increment based methods. Notable exceptions include the pioneering work of E. Imre Friedmann on cryptoendolithic lichens (0.6 g C/m²/y NPP) (Friedmann et al. 1993) and more recent surveys of coastal moss turfs (250 g C/m²/y NPP) (Pannewitz et al. 2005) and riparian Nostoc cyanobacterial mats (20 g C/m²/y NPP) (Novis et al. 2007). The availability of new approaches to directly measure photosynthetic activity (e.g. pulse amplitude modulated (PAM) fluorometry) provides a unique opportunity to compare productivity estimates among analytical approaches and refine our understanding of the energetic basis of dry valley foodwebs.

Here we present the results of a field survey in the McMurdo Dry Valleys where the important ecological functions of productivity and decomposition were examined along a broad environmental gradient previously demonstrated as an important driver of biotic diversity and activity (Geyer et al. 2013). PAM fluorometry was used to estimate primary productivity while exoenzyme activity assays provide an indication of detrital pathways and the
diversity of organic substrates. We discuss the overall significance of primary production within a low organic
matter ecosystem towards influencing subsurface processes and community structure, as well as promising avenues
for using PAM fluorometry in conjunction with other techniques to constrain rates of primary production (and its
sensitivity to environmental factors) within arid systems.

Site Description and Methods

Site Description

Surveys were conducted in Taylor Valley, a region well characterized by previous research within the
larger McMurdo Dry Valleys, Antarctica. Soils of this region are a poorly weathered, dry-permafrost composed of
>90% sand-sized particles with ice cement occurring within 0.5 m of the surface (Ugolini and Bockheim 2008).
Salinity and pH are generally high, a consequence of limited vertical water movement through soil layers that results
in the accumulation of weathered carbonates and aerially-deposited salts (Bockheim 1997). Low temperatures
restrict photosynthesis within this region to an approximately 6-8 week austral summer period when 24-hour
radiation elevates air and soil surface temperature (10°C and 25°C maxima, respectively) (Doran et al. 2002) and
stimulates the melting of ice and snow to yield free water. Cryotolerant organisms such as cyanobacterial mats are
reactivated and, in some cases, can resume photosynthesis and nitrogen fixation within minutes of rehydration along
the soil surface (Vincent and Howard-Williams 1986; McKnight et al. 2007). A surprisingly diverse assemblage of
microbes exists underground alongside a limited variety of metazoan invertebrates at higher trophic levels (Adams
et al. 2006; Takacs-Vesbach 2010).

Communities of cyanobacteria, moss, lichens, and eukaryotic algae are responsible for primary production
in this region and are often characterized by their niche habitat. For instance, a diversity of lithophytic cyanobacteria
(e.g. families Nostocaceae and Oscillatoriaceae) are commonly divided into the operational categories hypolithic,
endolithic, and epilithic according to the rock surface colonized (Broady 1996; Pointing et al. 2009). Cyanobacteria
and fewer than ten species of moss frequently form dense cryptogamic mats along the wetted soil margins of
streams, lakes, and snowpacks (Seppelt and Green 1998). A limited number of distinguishing morphological
characteristics makes in-field identification challenging, and thus most mat-forming colonies are identified by
morphotypes of color (e.g. black, orange, red) and/or physical location (e.g. wetted stream margin, submerged
aquatic) (Broady 1996; McKnight et al. 2007). The dominant soil bacterial phyla in this region include many of the
more common groups found worldwide, such as *Actinobacteria*, *Acidobacteria*, and *Bacteroidetes* (Cary et al. 2010).

Previous field surveys during the austral summer of 2010/2011 from Taylor and neighboring Wright Valleys indicated that soils associated with an *a priori* productivity gradient (defined by surface density of microbial mats) ranged over three orders of magnitude in chlorophyll *a* concentrations (0.30 - 270 µg/g dry material). Across this gradient was observed an increase in soil moisture, organic carbon, invertebrate abundance, microbial biomass carbon, and diversity of bacteria (Geyer et al. 2013; Ball and Virginia 2014). The activity of two common carbon-acquiring microbial exoenzymes (α- and β-glucosidase) were also positively associated with soil productivity, suggesting that productive habitats are more decompositionally active because of greater organic substrate concentrations, enhanced activity or biomass of decomposers, or perhaps both.

**Soil Sampling**

Here we report the results of continued sampling along this productivity gradient performed during the austral summer (January 2013) using five broad regions (Fig 1). These regions ranged from tens of meters to tens of kilometers apart and consisted of common soil habitats found in Taylor Valley such as stream margins, the wetted edge of snowpacks, and hyperarid soils (Table 1, Fig. 1). Although specific cryptogam identification was not determined, moss and/or cyanobacteria mats frequently colonized more productive soils but appeared absent in others. Three locations (2.5 m² each) were chosen to capture the range of visually apparent surface production within each of the five regions (15 locations overall); in so doing, soils along a productivity gradient were collected from both within each region and across the greater Taylor Valley. Locations of high productivity contained dense cryptogam mats up to 5 cm thick, while arid soils appeared barren and without conspicuous surface producers (Supplement 1). PAM measurements were made on light-adapted surfaces at eight equidistant points within each location following a gridded pattern. Triplicate soils were collected from within each location such that surface cryptogams were stored separately as replicates and subsurface soils (to a depth of 5 cm per pit) combined to produce one composite sample (~ 500 g) per location. Ten grams of soil from this composite sample was immediately preserved in a sucrose-lysis buffer for nucleic acid stabilization (Mitchell and Takacs-Vesbach 2008).

All samples were frozen at -20°C (molecular samples -80°C) within 48 hours of collection. Field sampling was permitted under McMurdo LTER NSF OPP grant 1115245.

**Biogeochemical and Molecular Analyses**
Surface cryptogam biomass was measured indirectly as chlorophyll $a$ concentrations via spectrophotometry from the acetone extract of dried surface soils (Castle et al. 2011; Geyer et al. 2013). Subsurface soil was 2 mm sieved and used for all subsequent analyses. Soil pH and electrical conductivity were measured from a 1:2 and 1:5 soil/water slurry, respectively, using standard procedures developed for this region (Nkem et al. 2006). Soil water content was determined gravimetrically by oven-drying for 48 hr at 105°C. Total nitrogen (TN) was estimated from ~300 mg of ground, dried, and acidified soil using a FlashEA 1112 NC Elemental Analyzer (CE Elantech, Lakewood, NJ, USA). Chloroform-labile carbon was used as an indication of soil microbial biomass carbon (MBC) where soil samples were fumigated with gaseous chloroform for five days under vacuum (Cheng and Virginia 1993). Paired fumigated and non-fumigated samples were then extracted with a 0.5M K$_2$SO$_4$ solution and final extracts analyzed for total organic carbon using a OI Model 1010 Total Organic Carbon Analyzer (OI Analytical, College Station, TX, USA), where final chloroform-labile carbon was calculated as the difference between fumigated and non-fumigated total organic carbon. Non-fumigated extracts were used as estimates of soluble soil organic carbon (SOC).

Potential soil extracellular enzyme activity was assayed for five carbon and nitrogen acquiring enzymes (Table 2) to characterize the diversity and magnitude of hydrolytic and oxidative decompositional pathways (Sinsabaugh and Shah 2011). These measures were also examined as an index of organic matter complexity (Tscherko et al. 2003). Hydrolytic activity was measured using 0.5 g soil incubations in the presence of labeled substrates and 50mM NaHCO$_3$ buffer (pH = 8.2) following the methods of Zeglin and others (2009). Oxidative assays underwent similar treatment, although standards were created by reacting a known mass of L-3,4-dihydroxyphenylalanine (L-DOPA) with horseradish peroxidase from which a standard curve (dilution series) of the product was used to infer activity within field samples. For all assays, triplicate samples were incubated at room temperature on a platform shaker (250 rpm) for a minimum of 2 hr and enzyme-induced fluorescence (hydrolytic enzymes) measured by excitation (365 nm) and emission (450 nm) or light absorbance (oxidative enzyme) measured by absorbance (460 nm) using a Tecan Infinite M200Pro plate reader (Tecan, Mannedorf, Zurich, Switzerland). In addition to sample incubations, control (buffer only), substrate (substrate + buffer), and standard (standard + buffer) references were analyzed to account for other sources of fluorescence. Final activity was normalized to sample microbial biomass carbon (MBC) and expressed as activity (nmol of substrate cleaved) h$^{-1}$ g MBC$^{-1}$. Organic substrate breakdown is assumed to be entirely the result of microbially exuded enzymes.
Bacterial diversity was estimated using a terminal restriction fragment length polymorphism (TRFLP) procedure, a conservative estimate of phylum level diversity (Thies 2007). DNA was extracted from soils using a modified cetyltrimethylammonium bromide (CTAB) procedure involving a mixture of 1% CTAB, 10% sodium dodecyl sulfate, phenol/chloroform/isoamyl alcohol (pH = 7.5), lysozyme (0.2 µg/µL), and proteinase K (20 µg/µL) with ~0.75 g soil. PCR amplification took place in triplicate using a standard 2 µL of diluted template, 0.025 units/µL of Taq Hot Start Polymerase (Promega Corporation, Madison, WI, USA), and the universal bacterial primers 8F (5'-AGAGTTTGATCMTGGCTCAG-3') and 519R (5'-ACCGCGGCTGCTGGCAC-3'), the forward primer labeled with a 5' 6-FAM fluorophore (Integrated DNA Technologies, Coralville, IA, USA). Amplification reaction conditions were previously optimized for these soils by Geyer and others (2013). Successful amplifications (13 of 15 samples) were digested with HaeIII (New England BioLabs, Ipswich, MA, USA) in triplicate for 3 hr at 37°C following manufacturer’s suggested protocols. Fragment separation/quantification took place in quadruplicate with an ABI 3130xl Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA) and fragments binned using the GeneMarker software AFLP protocol. Resulting sample profiles were standardized using the procedures outlined by Dunbar (2001) to produce both a consensus profile among replicates and final normalization of all sample profiles by total sample fluorescence.

**PAM Fluorometry**

A MINI-PAM (Walz) pulse amplitude modulated fluorometer was used to examine rates of surface cryptogam production in-situ for 12 locations. The PAM fluorometer uses saturating light to induce a measurable change in fluorescence directly proportional to the drop in photochemical quenching which results from the instantaneous light-induced reduction of the photosystem II (PSII) electron transport chain. The key measurements obtained from the PAM were effective quantum yield of PSII (YII) and electron transport rate (ETR). Additional measures of photon flux density (photosynthetically active radiation, or PAR) and temperature at the cryptogam surface were also recorded. YII is the proportion of incident light used to drive the photochemistry of photosynthesis (Ritchie and Bunthawin 2010), while ETR is derived from the product of YII, PAR, and two factors which account for a photon allocation factor between PSI and II (0.5) and a mean absorptance factor (0.84) previously described for a variety of plants.

\[
ETR (\mu\text{mol/m}^2/\text{s}) = \text{YII} \times \text{PAR} \times 0.5 \times 0.84
\]
ETR is thus an estimate of the rate of electron passage through PSII. Because four electrons pass through PSII per oxygen molecule produced during photosynthesis, estimates of gross photosynthesis (or more specifically, photosynthetic capacity) were calculated using (Figueroa et al. 2003; Ritchie and Bunthawin 2010):

\[
\text{GPP (\mu mol O}_2/\text{m}^2/\text{s)} = \frac{1}{4} \times \text{ETR}
\]

A strong linear relationship between ETR and gross photosynthesis has been previously demonstrated for Antarctic mosses (Green et al. 1998, Masojidek et al. 2000) and has been extrapolated to the cryptogams surveyed here. Being poikilohydric, the photosynthetic activity of Antarctic cryptogams is further constrained by moisture availability (Schroeter et al. 2011). Our seasonal estimates of GPP should thus be interpreted as simplifications that will require higher resolution moisture, temperature, and light conditions in order to be refined. All PAM measurements were auto-corrected for background fluorescence of non-biological material (e.g. rocks).

**Data Analysis**

Data analysis (correlation, t-tests, ANOVA, and simple/multiple linear regressions) was performed using SAS JMP. The normality of studentized residuals was examined and, if found significantly non-normal by Shapiro-Wilks test, either log\(_{10}\) (e.g. all enzyme activity values) or square-root transformed. Locations were clustered into three conservative productivity classes (e.g. low, intermediate, high) based on a k-means non-hierarchical clustering technique of soil moisture. Spearman correlation was used to assess pairwise interactions between all variables because of the presence of some nonlinear (monotonic) relationships. Multiple regression was performed using mixed stepwise selection of model parameters (\(\alpha = 0.15\)) that had variance inflation factors <10. Both TRFLP fragment abundances and enzyme activities were used in calculations of Shannon-Weiner diversity indexes. Enzyme diversity (Enz. H') calculations include the activity of AG, BG, NAG, and POX (Table 2) to provide a metric of carbon-acquiring enzyme activity from which the diversity of carbon substrates was inferred.

**Results**

Soil characteristics of the 15 locations sampled resemble those observed in previous work conducted in hydrological margins of streams and lacustrine environments of the McMurdo Dry Valleys (Barrett et al. 2009; Geyer et al. 2013) and captured gradients of gravimetric water content ranging over an order of magnitude (range = 1.3 – 17.3%; mean = 11.4%) and chlorophyll \(a\) concentrations over two orders of magnitude (range = 0.02 – 2.84 \(\mu g/g\) dry material; mean = 0.88 \(\mu g/g\) dry material). Molar C:N of total soil (range = 6.6 – 11.3; mean = 8.3) did not vary significantly with other measures of soil productivity. Correlational trends indicate that soil properties
associated with physicochemical severity (e.g., electrical conductivity and pH) are positively correlated with one another yet negatively correlated with properties of mesic, productive soils like chlorophyll $a$, microbial biomass carbon, and bacterial (TRFLP) diversity (Table 3). Because of its importance as a driver of most soil parameters in this arid system, soil moisture was chosen as a basis for clustering locations into three productivity zones (e.g. low, intermediate, high) to examine variability at this scale. Strong differences exist among productivity zones for many soil conditions such as pH and chlorophyll concentrations, and average values are reported per zone (Table 4).

PAM estimates of electron transport rate (ETR) were not significantly associated with soil moisture or chlorophyll $a$, although a positive trend did exist. ETR was significantly related to both PAR and temperature levels in a positive linear manner ($r^2 = 0.68, p < 0.001$; $r^2 = 0.24, p < 0.001$; Fig. 2). Although the relationship with PAR is largely expected (given that light intensity is a factor in calculating electron transport rate), both relationships are consistent in magnitude with the findings of Green and others (1998; 2002) for photobionts.

Soil enzyme activity varied significantly by location. POX and LAP (lignin- and protein-degrading enzymes, respectively) both exhibited a negative correlation with soil water content, as activity tended to be highest in the most arid habitats (Table 4). Activity of AG and BG (starch- and cellulose-degrading enzymes, respectively) had an opposite trend with the highest values found in productive soils, while NAG (chitin-degrading) activity exhibited no trend. An index of overall enzyme diversity was calculated using the Shannon-Weiner equation to highlight the relative change in evenness of carbon-acquiring enzyme activity (excluding protein-specific LAP), as described by Tscherko and others (2003). Enzyme diversity had a significant positive relationship with soil moisture ($r^2 = 0.34; p < 0.05$) and significant negative relationship with pH ($r^2 = 0.32; p < 0.05$). This result is a consequence of high POX activity (as indicated by the relative enzyme activity; Fig. 3) in arid soils, which is gradually replaced by a more even activity of all carbon-acquiring enzymes in productive soils. LAP activity did not correlate with total nitrogen concentrations, or either nitrate-N or ammonium-N (Supplement Data). Multiple regression results suggest soil water content as the driving force behind variation in most factors of biological diversity and activity (Fig 4).

**Discussion**

Environmental gradients are a key feature of arid environments often chosen for investigation as the inferred mechanism underlying spatial patterns between productivity, for example, and diversity (Noy-Meir 1973). While the diversity of microbial and metazoan communities in Antarctic terrestrial hotspots has been well characterized (Simmons et al. 2009; Zeglin et al. 2011; Niederberger et al. 2015), process based measurements like
primary productivity have received less attention. Here we contribute to this understanding of environmental
gradients by quantifying the rates of certain key functions that promote and reinforce the habitability of otherwise
hyperarid Antarctic soils.

PAM fluorometry was used to measure the rate of PSII electron transport rate (ETR), from which was
calculated gross primary production (GPP). GPP, organic carbon, and chlorophyll \( a \) all peaked in the wettest soils
that support the densest cryptogam mats. Average GPP was 6.97 \( \mu \text{mol } \text{O}_2/\text{m}^2/\text{s} \) in these most productive soils, with a
maximum of 17.74 \( \mu \text{mol } \text{O}_2/\text{m}^2/\text{s} \) for one location. Assuming a 50% respiratory carbon loss during fixation (i.e. net
primary productivity, NPP; Schlesinger 1997) and 60 days of productivity per year (Burkins et al. 2001), this is
equivalent to an average NPP rate of \( \sim 217 \; \text{g } \text{C}/\text{m}^2/\text{y} \) with a maximum of 552 g C/m\(^2\)/y. Considering that some soils
in Taylor Valley contain concentrations of organic matter approaching 250 g C/m\(^2\) (Moorhead et al. 2003), mean
residence time (pool/flux) of carbon in highly productive zones would equal \( \sim 2.2 \) years. This is substantially lower
than the average residence time of decades to centuries estimated for soil organic matter in the broader Taylor
Valley landscape (Burkins et al. 2001; Barrett et al. 2005). Organic matter of productive dry valley soils is thus
primarily labile photosynthates of recent origin that are rapidly utilized by soil decomposers; this situation is
reversed with soil aridity, however, as soil carbon becomes increasingly dominated by recalcitrant substrates of
ancient provenance (Burkins 2001).

Average GPP for the least productive soils was 0.27 \( \mu \text{mol } \text{O}_2/\text{m}^2/\text{s} \). Again assuming that half of gross
carbon and oxygen generation from GPP is consumed by respiration, this results in a NPP rate of 0.135 \( \mu \text{mol }
\text{O}_2/\text{m}^2/\text{s} \) (or 0.135 \( \mu \text{mol } \text{CO}_2/\text{m}^2/\text{s} \) of autotrophic respiration). This falls within the range of total soil respiration rates
previously described for arid dry valley soils (0.1-0.4 \( \mu \text{mol } \text{CO}_2/\text{m}^2/\text{s} \); Burkins et al. 2001; Parsons et al. 2004; Ball
et al. 2009) and suggests that autotrophic respiration could constitute a substantial portion of total soil respiration
even in arid soils. The consistency of these findings should encourage researchers to couple PAM fluorometry with
soil CO\(_2\) flux measurements in future work to attempt distinguishing rates of GPP, NPP, and respiration for producer
communities at higher spatial and temporal resolution (Pannewitz et al. 2006). Recent evidence has also suggested
that CO\(_2\) efflux measurements from dry mineral soils in this region may be at least partially abiotic in origin
(Shanhun et al. 2012; Ball and Virginia 2015), which underscores the limit of CO\(_2\) flux measurements to adequately
depict (on its own) biological activity for this region. PAM fluorometry yields independent measures of primary
production that can be used to further refine important properties of soil organic matter pools such as residence times.

Interestingly, while GPP inferred from PAM fluorometry appears to provide a valuable measure of soil productivity, it did not significantly correlate with chlorophyll levels (Table 3). This suggests that perhaps the better measure of soil productivity may ultimately depend on the temporal scale of inference. Concentrations of soil chlorophyll are thought to represent an integration of producer biomass accrual across days to weeks, from which can be inferred regular moisture availability and stable periods of producer growth. ETR and GPP values, however, provide rapid measures of producer performance under instantaneous light, temperature, and moisture conditions that may not necessarily correlate with chlorophyll concentrations. The sensitivity of producers to rapid environmental change, identification of potential production-limiting stressors, and repeated (non-invasive) long term measures of diel or even seasonal fluctuations in productivity of sample plots may be the best uses of PAM fluorometry. Indeed, previous work has applied PAM measures to reveal the effects of stress and damage to photosystem functioning (Schreiber 2004).

Patterns in enzyme activity across the productivity gradient indicate distinct shifts in the nature of detrital pathways as well as organic matter pool complexity. Arid locations exhibited low evenness in an index of carbon-acquiring enzyme diversity, as indicated by the overall dominance of phenol oxidase activity (Fig. 3). This evidence suggests the soil organic matter pool in arid zones may be primarily composed of recalcitrant materials targeted by oxidative enzymes. Although vascular (lignin-bearing) primary producers are absent from this system, recalcitrant compounds may originate from the fatty acids and proteins of decomposing moss and lichen tissue (Beyer et al. 1995) deposited during ancient high-stands of a proglacial lake during the Last Glacial Maximum in Taylor Valley (Hall et al. 2000). Such organic matter may be an important energetic source in the more hyperarid soils of this region (Barrett et al. 2006a). In a broader sense the activity of oxidative enzymes worldwide has been found to be greater in drier, more alkaline soils, perhaps a consequence of high mineral surface stability (Zeglin et al. 2009) or higher phenol solubility under such conditions (Sinsabaugh 2010). LAP was also relatively more active in arid rather than mesic locations, potentially indicating greater nitrogen limitation, reduced substrate (protein) availability, or potentially a higher enzyme reactive efficiency at increased pH as suggested by Sinsabaugh and others (2008).

Recalcitrant organic substrates that we suspect to predominate in these arid soils, together with low nitrogen
availability, likely contribute to the relatively low diversity and enzyme activity of microbial communities found in such habitats.

The relative activity of all carbon-acquiring enzymes (i.e. Enz. H') indicated a more even carbon-acquiring enzyme diversity within productive soils (Table 4). From this we infer higher diversity of organic compounds in more productive regions, a logical conclusion considering the presence of greater producer biomass and diversity (Orwin et al. 2006). Increased diversity of organic compounds may therefore be an additional factor behind the greater diversity of organotrophic bacterial communities in productive locations (Grayston et al. 1998). Niche differentiation among microorganisms for various substrates, particularly those that may be decomposed only via specialized enzymatic pathways, may be a mechanism (along with increased resource availability) responsible for increases in microbial diversity. Distinguishing the relative effects of resource quantity and quality remains an important direction for further research to establish important drivers of microbial community diversity.

The estimates of primary production we report, even within drier habitats, provide evidence that in-situ carbon fixation is occurring widely across the McMurdo Dry Valley landscape with likely effects on subsurface communities and biogeochemical rates. Environmental severity (soil pH, electrical conductivity) and resource availability (soil moisture, organic carbon concentration) vary inversely along a gradient of soil productivity and play important roles in determining biological diversity and activity, although moisture is the primary driver to explain community structure and function (Fig. 4). Changing enzyme activity along this gradient also highlights higher potential organic matter complexity in productive soils, an unforeseen factor that may promote microbial diversity. Our estimates for annual NPP of the most productive dry valley soils, colonized by mixed cyanobacteria and moss mats, indicate yields of ~217 g C/m²/y, only slightly less than estimates of 250 g C/m²/y for nearby coastal moss turfs (Pannewitz et al. 2005). We estimate annual NPP for the most arid soils (which dominate the dry valley landscape) to be ~8 g C/m²/y, and thus an average NPP for Taylor Valley soil productivity would be much lower than the global desert mean of 80 g C/m²/y (Waide et al. 1999). In spite of these low rates a diverse and active organotrophic community persists here, a testament to the strength of interaction between ecosystem functioning (production, decomposition), environmental conditions (resource quantity/quality), and biotic diversity.
Acknowledgments

We would like to thank the Crary Laboratory staff at McMurdo Station for their assistance, as well as Raytheon Company, Inc. and Petroleum Helicopters, Inc. for logistical support. We also thank Bobbie Niederlehner and several Virginia Tech collaborators for their contributions towards data acquisition and analysis.

References

Adams BJ, Bardgett RD, Ayres E, Wall DH, Aislabie J, Bamforth S, Bargagli R, Cary C, Cavacini P, Connell L, Convey P, Fell JW, Frati F, Hogg ID, Newsham KK, O'Donnell A, Russell N, Seppelt RD, and Stevens MI. 2006. Diversity and distribution of Victoria Land biota. Soil Biology & Biochemistry 38:3003-3018. 10.1016/j.soilbio.2006.04.030

Ball BA, and Virginia RA. 2014. The ecological role of moss in a polar desert: implications for aboveground-belowground and terrestrial-aquatic linkages. Polar Biology 37:651-664. 10.1007/s00300-014-1465-2

Ball BA, and Virginia RA. 2015. Controls on diel soil CO2 flux across moisture gradients in a polar desert. Antarctic Science 27:527-534. 10.1017/s0954102015000255

Barrett JE, Virginia RA, Barrett JE, Parsons AN, and Wall DH. 2009. Interactions between physical and biotic factors influence CO2 flux in Antarctic dry valley soils. Soil Biology & Biochemistry 41:1510-1517. 10.1016/j.soilbio.2009.04.011

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

Barrett JE, Virginia RA, Hopkins DW, Aislabie J, Bargagli R, Bockheim JG, Campbell IB, Lyons WB, Moorhead DL, Nkem JN, Sletten RS, Steltzer H, Wall DH, and Wallenstein MD. 2006a. Terrestrial ecosystem processes of Victoria Land, Antarctica. Soil Biology & Biochemistry 38:3019-3034. 10.1016/j.soilbio.2006.04.041

Barrett JE, Virginia RA, Parsons AN, and Wall DH. 2005. Potential soil organic matter turnover in Taylor Valley, Antarctica. Arctic Antarctic and Alpine Research 37:108-117.

Barrett JE, Virginia RA, Wall DH, Cary SC, Adams BJ, Hacker AL, and Aislabie JM. 2006b. Co-variation in soil biodiversity and biogeochemistry in northern and southern Victoria Land, Antarctica. Antarctic Science 18:535-548. 10.1017/s0954102006000587

Barrett JE, Virginia RA, Wall DH, Parsons AN, Powers LE, and Burkins MB. 2004. Variation in biogeochemistry and soil biodiversity across spatial scales in a polar desert ecosystem. Ecology (Washington D C) 85:3105-3118. 10.1890/03-0213

Beyer L, Sorge C, Blume HP, and Schulten HR. 1995. Soil organic matter composition and transformation in gelic histosols of coastal continental Antarctica. Soil Biology and Biochemistry 27:1279-1288. 10.1016/0038-0717(95)00054-1

Bockheim JG. 1997. Properties and classification of cold desert soils from Antarctica. Soil Science Society of America Journal 61:224-231.
Broady PA. 1996. Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and Conservation* 5:1307-1335.

Burkins MB, Virginia RA, and Wall DH. 2001. Organic carbon cycling in Taylor Valley, Antarctica: quantifying soil reservoirs and soil respiration. *Global Change Biology* 7:113-125.

Cary SC, McDonald IR, Barrett JE, and Cowan DA. 2010. On the rocks: the microbiology of Antarctic Dry Valley soils. *Nature Reviews Microbiology* 8:129-138. 10.1038/nrmicro2281

Castle SC, Morrison CD, and Barger NN. 2011. Extraction of chlorophyll a from biological soil crusts: A comparison of solvents for spectrophotometric determination. *Soil Biology & Biochemistry* 43:853-856. 10.1016/j.soilbio.2010.11.025

Chapin FS. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233-260.

Cheng W, and Virginia RA. 1993. Measurement of microbial biomass in Arctic tundra soils using fumigation-extraction and substrate-induced respiration procedures. *Soil Biology and Biochemistry* 25:135-141. 10.1016/0038-0717(93)90251-6

Doran PT, McKay CP, Clow GD, Dana GL, Fountain AG, Nylen T, and Lyons WB. 2002. Valley floor climate observations from the McMurdo dry valleys, Antarctica, 1986-2000. *Journal of Geophysical Research-Atmospheres* 107:art13. 10.1029/2001jd002045

Dunbar J, Ticknor LO, and Kuske CR. 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. 10.1128/aem.67.1.190-197.2001

Elberling B, Gregorich EG, Hopkins DW, Sparrow AD, Novis P, and Greenfield LG. 2006. Distribution and dynamics of soil organic matter in an Antarctic dry valley. *Soil Biology & Biochemistry* 38:3095-3106. 10.1016/j.soilbio.2005.12.011

Figuerola FL, Conde-Alvarez R, and Gomez I. 2003. Relations between electron transport rates determined by pulse amplitude modulated chlorophyll fluorescence and oxygen evolution in macroalgae under different light conditions. *Photosynthesis Research* 75:259-275. 10.1023/a:1023936313544

Friedmann EI, Kappen L, Meyer MA, and Nienow JA. 1993. Long-term productivity in the cryptoendolithic microbial community of the Ross Desert, Antarctica. *Microbial Ecology* 25:51-69.

Geyer KM, Altrichter AE, Van Horn DJ, Takacs-Vesbach CD, Gooseff MN, and Barrett JE. 2013. Environmental controls over bacterial communities in polar desert soils. *Ecosphere* 4:art127. 10.1890/es13-0048.1

Grayston SJ, Wang S, Campbell CD, and Edwards AC. 1998. Selective influence of plant species on microbial diversity in the rhizosphere. *Soil Biology and Biochemistry* 30:369-378. 10.1016/s0038-0717(97)00124-7

Green TGA, Schlensoog M, Sancho LG, Winkler JB, Broom FD, and Schroeter B. 2002. The photobiont determines the pattern of photosynthetic activity within a single lichen thallus containing cyanobacterial and green algal sectors (photosymbiomedeme). *Oecologia (Berlin)* 130:191-198.
Green TGA, Schroeter B, Kappen L, Seppelt RD, and Maseyk K. 1998. An assessment of the relationship between chlorophyll alpha fluorescence and CO2 gas exchange from field measurements on a moss and lichen. *Planta (Berlin)* 206:611-618. 10.1007/s004250050439

Hall BL, Denton GH, and Hendy CH. 2000. Evidence from Taylor Valley for a Grounded Ice Sheet in the Ross Sea, Antarctica. *Geografiska Annaler* 82:275-303.

Judd KE, Crump BC, and Kling GW. 2006. Variation in dissolved organic matter controls bacterial production and community composition. *Ecology* 87:2068-2079.

Lee CK, Barbier BA, Bottos EM, McDonald IR, and Cary SC. 2012. The Inter-Valley Soil Comparative Survey: the ecology of Dry Valley edaphic microbial communities. *Isme Journal* 6:1046-1057. 10.1038/ismej.2011.170

Lindeman RL. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-418. 10.2307/1930126

Masojidek J, Grobbelaar JU, Pechoar L, and Koblizek M. 2001. Photosystem II electron transport rates and oxygen production in natural waterblooms of freshwater cyanobacteria during a diel cycle. *Journal of Plankton Research* 23:57-66. 10.1093/plankt/23.1.57

McKnight DM, Tate CM, Andrews ED, Niyogi DK, Cozzetto K, Welch K, Lyons WB, and Capone DG. 2007. Reactivation of a cryptobiotic stream ecosystem in the McMurdo Dry Valleys, Antarctica: A long-term geomorphological experiment. *Geomorphology* 89:186-204. 10.1016/j.geomorph.2006.07.025

McNaughton S, Oesterheld M, Frank D, and Williams K. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature (London)* 341:142-144.

Mitchell KR, and Takacs-Vesbach CD. 2008. A comparison of methods for total community DNA preservation and extraction from various thermal environments. *Journal of Industrial Microbiology & Biotechnology* 35:1139-1147. 10.1007/s10295-008-0393-y

Moorhead DL, Barrett JE, Virginia RA, Wall DH, and Porazinska D. 2003. Organic matter and soil biota of upland wetlands in Taylor Valley, Antarctica. *Polar Biology* 26:567-576. 10.1007/s00300-003-0524-x

Niederberger TD, Sohm JA, Gunderson TE, Parker AE, Tirindelli J, Capone DG, Carpenter EJ, and Cary SC. 2015. Microbial community composition of transiently wetted Antarctic Dry Valley soils. *Frontiers in Microbiology* 6:12. 10.3389/fmicb.2015.00009

Nkem JN, Virginia RA, Barrett JE, Wall DH, and Li G. 2006. Salt tolerance and survival thresholds for two species of Antarctic soil nematodes. *Polar Biology* 29:643-651. 10.1007/s00300-005-0101-6

Novis PM, Whitehead D, Gregorich EG, Hunt JE, Sparrow AD, Hopkins DW, Elberling B, and Greenfield LG. 2007. Annual carbon fixation in terrestrial populations of Nostoc commune (Cyanobacteria) from an Antarctic dry valley is driven by temperature regime. *Global Change Biology* 13:1224-1237. 10.1111/j.1365-2486.2007.01354.x

Noy-Meir I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.
Orwin KH, Wardle DA, and Greenfield LG. 2006. Ecological consequences of carbon substrate identity and diversity in a laboratory study. *Ecology (Washington D C)* 87:580-593. 10.1890/05-0383

Pannewitz S, Green TGA, Maysek K, Schlenosg M, Seppelt R, Sancho LG, Turk R, and Schroeter B. 2005. Photosynthetic responses of three common mosses from continental Antarctica. *Antarctic Science* 17:341-352. 10.1017/s0954102005002774

Pannewitz S, Green TGA, Schlenosg M, Seppelt R, Sancho LG, and Schroeter B. 2006. Photosynthetic performance of Xanthoria mawsonii C.W. Dodge in coastal habitats, Ross Sea region, continental Antarctica. *Lichenologist (London)* 38:67-81. 10.1017/s0024282905005384

Parsons AN, Barrett JE, Wall DH, and Virginia RA. 2004. Soil carbon dioxide flux in Antarctic dry valley ecosystems. *Ecosystems* 7:286-295. 10.1007/s10021-003-0132-1

Pointing SB, Chan YK, Lacap DC, Lau MCY, Jurgens JA, and Farrell RL. 2009. Highly specialized microbial diversity in hyper-arid polar desert. *Proceedings of the National Academy of Sciences of the United States of America* 106:19964-19969. 10.1073/pnas.0908274106

Ritchie RJ, and Bunthawin S. 2010. The use of pulse amplitude modulation (PAM) fluorometry to measure photosynthesis in a cam orchid, Dendrobium spp. (D. CV. Viravuth Pink). *International Journal of Plant Sciences* 171:575-585. 10.1086/653131

Schlesinger WH. 1997. The Biosphere: The carbon cycle of terrestrial ecosystems. In: Schlesinger, WH, ed. Biogeochemistry. San Diego: Elsevier Science, 127-165.

Schreiber U. 2004. Pulse-Amplitude-Modulation (PAM) Fluorometry and Saturation Pulse Method: An Overview. Chlorophyll a fluorescence: A signature of photosynthesis (BOOK).

Schroeter B, Green TGA, Pannewitz S, Schlenosg M, and Sancho LG. 2011. Summer variability, winter dormancy: lichen activity over 3 years at Botany Bay, 77 degrees S latitude, continental Antarctica. *Polar Biology* 34:13-22. 10.1007/s00300-010-0851-7

Seppelt RD, and Green TGA. 1998. A bryophyte flora for Southern Victoria Land, Antarctica. *New Zealand Journal of Botany* 36:617-635.

Shanhun FL, Almond PC, Clough TJ, and Smith CMS. 2012. Abiotic processes dominate CO2 fluxes in Antarctic soils. *Soil Biology & Biochemistry* 53:99-111. 10.1016/j.soilbio.2012.04.027

Simmons BL, Wall DH, Adams BI, Ayres E, Barrett JE, and Virginia RA. 2009. Terrestrial mesofauna in above- and below-ground habitats: Taylor Valley, Antarctica. *Polar Biology* 32:1549-1558. 10.1007/s00300-009-0639-9

Sinsabaugh RL. 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. *Soil Biology & Biochemistry* 42:391-404. 10.1016/j.soilbio.2009.10.014

Sinsabaugh RL, J. Shah. 2011. Ecoenzymatic stoichiometry of recalcitrant organic matter decomposition: the growth rate hypothesis in reverse. *Biogeochemistry* 102:31-43.
Sinsabaugh RL, Lauber CL, Weintraub MN, Ahmed B, Allison SD, Crenshaw C, Contosta AR, Cusack D, Frey S, Gallo ME, Gartner TB, Hobbie SE, Holland K, Keeler BL, Powers JS, Stursova M, Takacs-Vesbach C, Waldrop MP, Wallenstein MD, Zak DR, and Zeglin LH. 2008. Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* 11:1252-1264. 10.1111/j.1461-0248.2008.01245.x

Takacs-Vesbach CD. 2010. Factors promoting microbial diversity in the McMurdo Dry Valleys, Antarctica.

Astrobiology series.

Thies JE. 2007. Soil microbial community analysis using terminal restriction fragment length polymorphisms. *Soil Science Society of America Journal* 71:579-591. 10.2136/sssaj2006.0318

Tilman D. 1982. Resource competition and community structure. Monographs in population biology.

Treonis AM, Wall DH, and Virginia RA. 1999. Invertebrate biodiversity in Antarctic dry valley soils and sediments. *Ecosystems* 2:482-492.

Tscherko D, Rustemeier J, Richter A, Wanek W, and Kandeler E. 2003. Functional diversity of the soil microflora in primary succession across two glacier forelands in the Central Alps. *European Journal of Soil Science* 54:685-696. 10.1046/j.1351-0754.2003.0570.x

Ugolini FC, and Bockheim JG. 2008. Antarctic soils and soil formation in a changing environment: A review. *Geoderma* 144:1-8. 10.1016/j.geoderma.2007.10.005

Vincent WF, and Howard-Williams C. 1986. Antarctic stream ecosystems - Physiological ecology of a blue-green algal epilithon. *Freshwater Biology* 16:219-233. 10.1111/j.1365-2427.1986.tb00966.x

Virginia RA, and Wall DH. 1999. How soils structure communities in the Antarctic dry valleys. *Bioscience* 49:973-983.

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, and Parmenter R. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257-300. 10.1146/annurev.ecolsys.30.1.257

Zeglin LH, Dahm CN, Barrett JE, Gooseff MN, Fitpatrick SK, and Takacs-Vesbach CD. 2011. Bacterial Community Structure Along Moisture Gradients in the Parafuvial Sediments of Two Ephemeral Desert Streams. *Microbial Ecology* 61:543-556. 10.1007/s00248-010-9782-7

Zeglin LH, Sinsabaugh RL, Barrett JE, Gooseff MN, and Takacs-Vesbach CD. 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. 10.1007/s10021-009-9242-8
Table 1. Description of the five sampling regions from which three locations (each) were chosen to collect samples. Locations within each region were chosen to capture the range of soil primary productivity visually apparent.

| Region | Landscape location | Latitude/longitude (decimal degree) | Elevation (m above sea level) |
|--------|--------------------|-------------------------------------|-----------------------------|
| 1      | Bonney Riegel, near Wormherder Creek | -77.733333/162.320183 | 294.5 |
| 2      | Bonney Riegel, near Wormherder Creek | -77.730383/162.334400 | 259.9 |
| 3      | Snowpack margin, near south shore Lake Hoare | -77.637333/162.881200 | 151.0 |
| 4      | Upper Green Creek margin | -77.624400/163.05403 | 18.1 |
| 5      | Canada Stream margin | -77.615417/163.041450 | 42.9 |
Table 2. Additional information for enzymatic assays of soils. Standards for the phenol oxidase assay were created by reacting a known mass of L-3,4-dihydroxyphenylalanine substrate with a horseradish peroxidase. 4-MUB = 4-methylumbelliferyl.

| Enzyme                        | Shorthand | Activity | Substrate                        | Standard | Target  |
|-------------------------------|-----------|----------|----------------------------------|----------|---------|
| α-glucosidase                 | AG        | hydrolytic | 4-MUB-α-D-glucopyranoside         | 4-MUB    | starch  |
| β-glucosidase                 | BG        | hydrolytic | 4-MUB-β-D-glucopyranoside         | 4-MUB    | cellulose |
| N-acetyl-β-glucosaminidase    | NAG       | hydrolytic | 4-MUB-N-acetyl-β-D-glucosaminide  | 4-MUB    | chitin  |
| phenol oxidase                | POX       | oxidative | L-3,4-dihydroxyphenylalanine      | N/A      | lignin  |
| leucine aminopeptidase        | LAP       | hydrolytic | L-leucine-7-amido-4-methylcoumarin HCl | 7-amino-4-methylcoumarin | protein |
Table 3. Spearman correlation matrix for soil properties. Electrical conductivity (EC, μS/cm); chlorophyll a (Chl a, μg/g dry soil); gravimetric moisture (% Moist); soil organic carbon (SOC, mg/kg dry soil); total nitrogen (TN, mg/kg dry soil); microbial biomass carbon (MBC, mg/kg dry soil); TRFLP bacterial diversity (Bact. H'); α-glucosidase activity (AG, nmol/g MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr); diversity index of activity for carbon-acquiring enzymes (Enz. H'); electron transport rate (ETR, μmol/m²/s).

| Variable | pH | EC | Chl a | % Moist | SOC | TN | MBC | Bact. H' | AG | POX | Enz. H' |
|----------|----|----|--------|---------|-----|----|------|--------|-----|-----|--------|
| ETR      |    |    |        |         |     |    |      |        |     |     |        |
| Enz. H'  |    |    |        |         |     |    |      |        |     |     |        |
| POX      |    |    |        |         |     |    |      |        |     |     |        |
| AG       |    |    |        |         |     |    |      |        |     |     |        |
| MBC      |    |    |        |         |     |    |      |        |     |     |        |
| SOC      |    |    |        |         |     |    |      |        |     |     |        |
| TN       |    |    |        |         |     |    |      |        |     |     |        |
| % Moist  |    |    |        |         |     |    |      |        |     |     |        |
| Chl a    |    |    |        |         |     |    |      |        |     |     |        |
| EC       |    |    |        |         |     |    |      |        |     |     |        |
| % Moist  |    |    |        |         |     |    |      |        |     |     |        |
| SOC      |    |    |        |         |     |    |      |        |     |     |        |
| TN       |    |    |        |         |     |    |      |        |     |     |        |
| MBC      |    |    |        |         |     |    |      |        |     |     |        |
| Bact. H' |    |    |        |         |     |    |      |        |     |     |        |
| AG       |    |    |        |         |     |    |      |        |     |     |        |
| POX      |    |    |        |         |     |    |      |        |     |     |        |
| Enz. H'  |    |    |        |         |     |    |      |        |     |     |        |

* p < 0.05; ** p < 0.01; *** p < 0.001
Table 4. Average (untransformed) edaphic properties for 15 soil habitats clustered by three productivity zones.

Standard error in parentheses except when missing data reduced $n < 3$ (NA). Lowercase letters indicate significant difference by ANOVA ($p < 0.05$). Electrical conductivity (EC, µS/cm); chlorophyll $a$ (Chl$a$, µg/g dry soil); gravimetric moisture (% Moist); soil organic carbon (SOC, mg/kg dry soil); total nitrogen (TN, mg/kg dry soil); microbial biomass carbon (MBC, mg/kg dry soil); TRFLP bacterial diversity (Bact. $H'$); $\alpha$-glucosidase activity (AG, nmol/g MBC/hr); $\beta$-glucosidase activity (BG, nmol/g MBC/hr); N-acetyl-$\beta$-glucosaminidase activity (NAG, nmol/g MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr); leucine aminopeptidase activity (LAP, nmol/g MBC/hr); carbon-acquiring enzyme diversity (Enz. $H'$); electron transport rate (ETR, µmol/m$^2$/s); gross primary production (GPP, µmol O$_2$/m$^2$/s).

| Variable       | Low ($n = 3$) | Intermediate ($n = 7$) | High ($n = 5$) |
|----------------|---------------|------------------------|---------------|
| pH             | 8.77a (0.04)  | 8.75a (0.04)           | 8.5b (0.07)   |
| EC             | 99.57a (35.76)| 54.6ab (7.49)          | 26.56b (6.14) |
| Chla           | 0.08a (0.05)  | 0.73ab (0.23)          | 1.56b (0.39)  |
| % Moist        | 3.94a (1.28)  | 11.51b (0.73)          | 15.85c (0.56) |
| SOC            | 234.15a (29.87)| 418.03a (82.88)       | 438.71a (104.03)|
| TN             | 34.66a (3.98) | 55.34a (9.71)          | 61.00a (13.26)|
| MBC            | 7.44a (2.23)  | 12.93a (2.66)          | 15.57a (3.49) |
| Bact. $H'$     | 4.06a (NA)    | 4.23a (0.05)           | 4.27a (0.05)  |
| AG             | 6005a (1987)  | 9783a (2279)           | 14767a (3505) |
| BG             | 7233a (988)   | 15048ab (3020)         | 25194b (3621) |
| NAG            | 1633a (415)   | 2028a (272)            | 2502a (316)   |
| POX            | 2.51x10$^7$a (9.33x10$^6$) | 1.13x10$^7$a (1.70x10$^6$) | 1.00x10$^7$a (2.18x10$^6$) |
| LAP            | 1.26x10$^9$a (2.30x10$^8$) | 9.86x10$^9$a (1.77x10$^9$) | 8.48x10$^9$a (1.30x10$^9$) |
| Enz. $H'$      | 0.007a (0.009)| 0.020ab (0.006)        | 0.039b (0.007) |
| ETR            | 1.06a (NA)    | 19.21a (9.14)          | 27.86a (11.06) |
| GPP            | 0.27a (NA)    | 4.80a (2.3)            | 6.97a (2.8)   |
**Fig. 1.** Location of the five regional sampling sites in Taylor Valley of the McMurdo Dry Valleys, Antarctica.
Fig. 2. Linear relationship between electron transport rate (ETR) and the density of photosynthetically active radiation (PAR) (a) and temperature (b).
Fig. 3. Relative activity of five standardized ((x-mean)/standard deviation + 3) exoenzymes for sample locations clustered into three productivity classes by soil moisture content. The number of observations are \( n = 3 \) (Low), \( n = 7 \) (Intermediate), and \( n = 5 \) (High). \( \alpha \)-glucosidase activity (AG, nmol/g MBC/hr); \( \beta \)-glucosidase activity (BG, nmol/g MBC/hr); N-acetyl-\( \beta \)-glucosaminidase activity (NAG, nmol/g MBC/hr); leucine aminopeptidase activity (LAP, nmol/g MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr).
Fig. 4. Simple linear regression (SLR, $r^2$) results (a) of soil factors against parameters associated with resource availability (e.g. % gravimetric moisture, chlorophyll $a$) and environmental severity (e.g. pH, electrical conductivity). Shaded cells indicate a negative relationship for simple regressions. Multiple linear regression (MLR, $R^2$) results indicate parameter(s) that best predicts soil factors. Illustration of SLR results (b) along a hypothetical environmental gradient. Gravimetric moisture (% Moist); electrical conductivity (EC, $\mu$S/cm); chlorophyll $a$ (Chl $a$, $\mu$g/g dry soil); $\alpha$-glucosidase activity (AG, nmol/g MBC/hr); $\beta$-glucosidase activity (BG, nmol/g MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr); leucine aminopeptidase activity (LAP, nmol/g MBC/hr); index of activity for all carbon-acquiring enzymes (Enz. H'); TRFLP bacterial diversity (Bact. H'); gross primary production (GPP, $\mu$mol O$_2$/m$^2$/s).