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

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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 $O_2/m^2/s$ in the most arid soils to an average of 6.97 μmol $O_2/m^2/s$ in the most productive soils, the latter equivalent to 217 g $C/m^2/y$ 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.

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2   **desert ecosystem**

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18   **Abstract**

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22   availability) and geochemical severity (e.g. pH, electrical conductivity). In the McMurdo Dry Valleys of Antarctica,
23   environmental gradients determine numerous properties of soil communities and yet relatively few estimates of
24   gross or net primary productivity (GPP, NPP) exist for this region. Here we describe a survey utilizing pulse
25   amplitude modulation (PAM) fluorometry to estimate rates of GPP across a broad environmental gradient along
26   with belowground microbial diversity and decomposition. PAM estimates of GPP ranged from an average of 0.27
27   μmol O_2/m^2/s in the most arid soils to an average of 6.97 μmol O_2/m^2/s in the most productive soils, the latter
28   equivalent to 217 g C/m^2/y in annual net primary production assuming a 60 day growing season. A diversity index
29   of four carbon-acquiring enzyme activities also increased with soil productivity, suggesting that the diversity of
30   organic substrates in mesic environments may be an additional driver of microbial diversity. Overall, soil
31   productivity was a stronger predictor of microbial diversity and enzymatic activity than any estimate of geochemical
32   severity. These results highlight the fundamental role of environmental gradients to control community diversity and
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Introduction

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/m^2/y NPP) (Friedmann et al. 1993) and more recent surveys of coastal moss turfs (250 g C/m^2/y NPP) (Pannewitz et al. 2005) and riparian *Nostoc* cyanobacterial mats (20 g C/m^2/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

85   diversity of organic substrates. We discuss the overall significance of primary production within a low organic

86   matter ecosystem towards influencing subsurface processes and community structure, as well as promising avenues

87   for using PAM fluorometry in conjunction with other techniques to constrain rates of primary production (and its

88   sensitivity to environmental factors) within arid systems.

89   **Site Description and Methods**

90   *Site Description*

91   Surveys were conducted in Taylor Valley, a region well characterized by previous research within the

92   larger McMurdo Dry Valleys, Antarctica. Soils of this region are a poorly weathered, dry-permafrost composed of

93   >90% sand-sized particles with ice cement occurring within 0.5 m of the surface (Ugolini and Bockheim 2008).

94   Salinity and pH are generally high, a consequence of limited vertical water movement through soil layers that results

95   in the accumulation of weathered carbonates and aerially-deposited salts (Bockheim 1997). Low temperatures

96   restrict photosynthesis within this region to an approximately 6-8 week austral summer period when 24-hour

97   radiation elevates air and soil surface temperature (10°C and 25°C maxima, respectively) (Doran et al. 2002) and

98   stimulates the melting of ice and snow to yield free water. Cryotolerant organisms such as cyanobacterial mats are

99   reactivated and, in some cases, can resume photosynthesis and nitrogen fixation within minutes of rehydration along

100   the soil surface (Vincent and Howard-Williams 1986; McKnight et al. 2007). A surprisingly diverse assemblage of

101   microbes exists underground alongside a limited variety of metazoan invertebrates at higher trophic levels (Adams

102   et al. 2006; Takacs-Vesbach 2010).

103   Communities of cyanobacteria, moss, lichens, and eukaryotic algae are responsible for primary production

104   in this region and are often characterized by their niche habitat. For instance, a diversity of lithophytic cyanobacteria

105   (e.g. families *Nostocaceae* and *Oscillatoriaceae*) are commonly divided into the operational categories hypolithic,

106   endolithic, and epilithic according to the rock surface colonized (Broady 1996; Pointing et al. 2009). Cyanobacteria

107   and fewer than ten species of moss frequently form dense cryptogamic mats along the wetted soil margins of

108   streams, lakes, and snowpacks (Seppelt and Green 1998). A limited number of distinguishing morphological

109   characteristics makes in-field identification challenging, and thus most mat-forming colonies are identified by

110   morphotypes of color (e.g. black, orange, red) and/or physical location (e.g. wetted stream margin, submerged

111   aquatic) (Broady 1996; McKnight et al. 2007). The dominant soil bacterial phyla in this region include many of the

112   more common groups found worldwide, such as *Actinobacteria*, *Acidobacteria*, and *Bacteroidetes* (Cary et al.

113   2010).

114   Previous field surveys during the austral summer of 2010/2011 from Taylor and neighboring Wright

115   Valleys indicated that soils associated with an *a priori* productivity gradient (defined by surface density of microbial

116   mats) ranged over three orders of magnitude in chlorophyll *a* concentrations (0.30 - 270 μg/g dry material). Across

117   this gradient was observed an increase in soil moisture, organic carbon, invertebrate abundance, microbial biomass

118   carbon, and diversity of bacteria (Geyer et al. 2013; Ball and Virginia 2014). The activity of two common carbon-

119   acquiring microbial exoenzymes (α- and β-glucosidase) were also positively associated with soil productivity,

120   suggesting that productive habitats are more decompositionally active because of greater organic substrate

121   concentrations, enhanced activity or biomass of decomposers, or perhaps both.

122   *Soil Sampling*

123   Here we report the results of continued sampling along this productivity gradient performed during the

124   austral summer (January 2013) using five broad regions (Fig 1). These regions ranged from tens of meters to tens of

125   kilometers apart and consisted of common soil habitats found in Taylor Valley such as stream margins, the wetted

126   edge of snowpacks, and hyperarid soils (Table 1, Fig. 1). Although specific cryptogam identification was not

127   determined, moss and/or cyanobacteria mats frequently colonized more productive soils but appeared absent in

128   others. Three locations (2.5 m^2 each) were chosen to capture the range of visually apparent surface production

129   within each of the five regions (15 locations overall); in so doing, soils along a productivity gradient were collected

130   from both within each region and across the greater Taylor Valley. Locations of high productivity contained dense

131   cryptogam mats up to 5 cm thick, while arid soils appeared barren and without conspicuous surface producers

132   (Supplement 1). PAM measurements were made on light-adapted surfaces at eight equidistant points within each

133   location following a gridded pattern. Triplicate soils were collected from within each location such that surface

134   cryptogams were stored separately as replicates and subsurface soils (to a depth of 5 cm per pit) combined to

135   produce one composite sample (~ 500 g) per location. Ten grams of soil from this composite sample was

136   immediately preserved in a sucrose-lysis buffer for nucleic acid stabilization (Mitchell and Takacs-Vesbach 2008).

137   All samples were frozen at -20°C (molecular samples -80°C) within 48 hours of collection. Field sampling was

138   permitted under McMurdo LTER NSF OPP grant 1115245.

139   *Biogeochemical and Molecular Analyses*

140   Surface cryptogam biomass was measured indirectly as chlorophyll *a* concentrations via spectrophotometry

141   from the acetone extract of dried surface soils (Castle et al. 2011; Geyer et al. 2013). Subsurface soil was 2 mm

142   sieved and used for all subsequent analyses. Soil pH and electrical conductivity were measured from a 1:2 and 1:5

143   soil/water slurry, respectively, using standard procedures developed for this region (Nkem et al. 2006). Soil water

144   content was determined gravimetrically by oven-drying for 48 hr at 105°C. Total nitrogen (TN) was estimated from

145   ~300 mg of ground, dried, and acidified soil using a FlashEA 1112 NC Elemental Analyzer (CE Elantech,

146   Lakewood, NJ, USA). Chloroform-labile carbon was used as an indication of soil microbial biomass carbon (MBC)

147   where soil samples were fumigated with gaseous chloroform for five days under vacuum (Cheng and Virginia

148   1993). Paired fumigated and non-fumigated samples were then extracted with a 0.5M K_2SO_4 solution and final

149   extracts analyzed for total organic carbon using a OI Model 1010 Total Organic Carbon Analyzer (OI Analytical,

150   College Station, TX, USA), where final chloroform-labile carbon was calculated as the difference between

151   fumigated and non-fumigated total organic carbon. Non-fumigated extracts were used as estimates of soluble soil

152   organic carbon (SOC).

153   Potential soil extracellular enzyme activity was assayed for five carbon and nitrogen acquiring enzymes

154   (Table 2) to characterize the diversity and magnitude of hydrolytic and oxidative decompositional pathways

155   (Sinsbaugh and Shah 2011). These measures were also examined as an index of organic matter complexity

156   (Tscherko et al. 2003). Hydrolytic activity was measured using 0.5 g soil incubations in the presence of labeled

157   substrates and 50mM $NaHCO_3$ buffer (pH = 8.2) following the methods of Zeglin and others (2009). Oxidative

158   assays underwent similar treatment, although standards were created by reacting a known mass of L-3,4-

159   dihydroxyphenylalanine (L-DOPA) with horseradish peroxidase from which a standard curve (dilution series) of the

160   product was used to infer activity within field samples. For all assays, triplicate samples were incubated at room

161   temperature on a platform shaker (250 rpm) for a minimum of 2 hr and enzyme-induced fluorescence (hydrolytic

162   enzymes) measured by excitation (365 nm) and emission (450 nm) or light absorbance (oxidative enzyme) measured

163   by absorbance (460 nm) using a Tecan Infinite M200Pro plate reader (Tecan, Mannedorf, Zurich, Switzerland). In

164   addition to sample incubations, control (buffer only), substrate (substrate + buffer), and standard (standard + buffer)

165   references were analyzed to account for other sources of fluorescence. Final activity was normalized to sample

166   microbial biomass carbon (MBC) and expressed as activity (nmol of substrate cleaved) h^{-1} g MBC^{-1}. Organic

167   substrate breakdown is assumed to be entirely the result of microbially exuded enzymes.

168   Bacterial diversity was estimated using a terminal restriction fragment length polymorphism (TRFLP)

169   procedure, a conservative estimate of phylum level diversity (Thies 2007). DNA was extracted from soils using a

170   modified cetyltrimethylammonium bromide (CTAB) procedure involving a mixture of 1% CTAB, 10% sodium

171   dodecyl sulfate, phenol/chloroform/isoamyl alcohol (pH = 7.5), lysozyme (0.2 µg/µL), and proteinase K (20 µg/µL)

172   with ~0.75 g soil. PCR amplification took place in triplicate using a standard 2 µL of diluted template, 0.025

173   units/µL of Taq Hot Start Polymerase (Promega Corporation, Madison, WI, USA), and the universal bacterial

174   primers 8F (5'-AGAGTTTGATCMTGGCTCAG-3') and 519R (5'-ACCGCGGCTGCTGGCAC-3'), the forward

175   primer labeled with a 5' 6-FAM fluorophore (Integrated DNA Technologies, Coralville, IA, USA). Amplification

176   reaction conditions were previously optimized for these soils by Geyer and others (2013). Successful amplifications

177   (13 of 15 samples) were digested with HaeIII (New England BioLabs, Ipswich, MA, USA) in triplicate for 3 hr at

178   37°C following manufacturer's suggested protocols. Fragment separation/quantification took place in quadruplicate

179   with an ABI 3130xl Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA) and fragments binned using the

180   GeneMarker software AFLP protocol. Resulting sample profiles were standardized using the procedures outlined by

181   Dunbar (2001) to produce both a consensus profile among replicates and final normalization of all sample profiles

182   by total sample fluorescence.

183   *PAM Fluorometry*

184   A MINI-PAM (Walz) pulse amplitude modulated fluorometer was used to examine rates of surface

185   cryptogam production *in-situ* for 12 locations. The PAM fluorometer uses saturating light to induce a measurable

186   change in fluorescence directly proportional to the drop in photochemical quenching which results from the

187   instantaneous light-induced reduction of the photosystem II (PSII) electron transport chain. The key measurements

188   obtained from the PAM were effective quantum yield of PSII (YII) and electron transport rate (ETR). Additional

189   measures of photon flux density (photosynthetically active radiation, or PAR) and temperature at the cryptogam

190   surface were also recorded. YII is the proportion of incident light used to drive the photochemistry of photosynthesis

191   (Ritchie and Bunthawin 2010), while ETR is derived from the product of YII, PAR, and two factors which account

192   for a photon allocation factor between PSI and II (0.5) and a mean absorptance factor (0.84) previously described for

193   a variety of plants.

194    $$\text{ETR (µmol/m}^2\text{/s)} = \text{YII} \times \text{PAR} \times 0.5 \times 0.84$$

195 ETR is thus an estimate of the rate of electron passage through PSII. Because four electrons pass through PSII per

196 oxygen molecule produced during photosynthesis, estimates of gross photosynthesis (or more specifically,

197 photosynthetic capacity) were calculated using (Figueroa et al. 2003; Ritchie and Bunthawin 2010):

$$\text{GPP } (\mu\text{mol O}_2/\text{m}^2/\text{s}) = 1/4 \text{ x ETR}$$

199 A strong linear relationship between ETR and gross photosynthesis has been previously demonstrated for Antarctic

200 mosses (Green et al. 1998, Masojidek et al. 2000) and has been extrapolated to the cryptogams surveyed here. Being

201 poikilohydric, the photosynthetic activity of Antarctic cryptogams is further constrained by moisture availability

202 (Schroeter et al. 2011). Our seasonal estimates of GPP should thus be interpreted as simplifications that will require

203 higher resolution moisture, temperature, and light conditions in order to be refined. All PAM measurements were

204 auto-corrected for background fluorescence of non-biological material (e.g. rocks).

205 *Data Analysis*

206 Data analysis (correlation, t-tests, ANOVA, and simple/multiple linear regressions) was performed using

207 SAS JMP. The normality of studentized residuals was examined and, if found significantly non-normal by Shapiro-

208 Wilks test, either $\log_{10}$ (e.g. all enzyme activity values) or square-root transformed. Locations were clustered into

209 three conservative productivity classes (e.g. low, intermediate, high) based on a k-means non-hierarchical clustering

210 technique of soil moisture. Spearman correlation was used to assess pairwise interactions between all variables

211 because of the presence of some nonlinear (monotonic) relationships. Multiple regression was performed using

212 mixed stepwise selection of model parameters ($\alpha = 0.15$) that had variance inflation factors <10. Both TRFLP

213 fragment abundances and enzyme activities were used in calculations of Shannon-Weiner diversity indexes. Enzyme

214 diversity (Enz. H') calculations include the activity of AG, BG, NAG, and POX (Table 2) to provide a metric of

215 carbon-acquiring enzyme activity from which the diversity of carbon substrates was inferred.

216 **Results**

217 Soil characteristics of the 15 locations sampled resemble those observed in previous work conducted in

218 hydrological margins of streams and lacustrine environments of the McMurdo Dry Valleys (Barrett et al. 2009;

219 Geyer et al. 2013) and captured gradients of gravimetric water content ranging over an order of magnitude (range =

220 1.3 – 17.3%; mean = 11.4%) and chlorophyll *a* concentrations over two orders of magnitude (range = 0.02 – 2.84

221 ug/g dry material; mean = 0.88 µg/g dry material). Molar C:N of total soil (range = 6.6 – 11.3; mean = 8.3) did not

222 vary significantly with other measures of soil productivity. Correlational trends indicate that soil properties

223   associated with physicochemical severity (e.g., electrical conductivity and pH) are positively correlated with one

224   another yet negatively correlated with properties of mesic, productive soils like chlorophyll *a*, microbial biomass

225   carbon, and bacterial (TRFLP) diversity (Table 3). Because of its importance as a driver of most soil parameters in

226   this arid system, soil moisture was chosen as a basis for clustering locations into three productivity zones (e.g. low,

227   intermediate, high) to examine variability at this scale. Strong differences exist among productivity zones for many

228   soil conditions such as pH and chlorophyll concentrations, and average values are reported per zone (Table 4).

229   PAM estimates of electron transport rate (ETR) were not significantly associated with soil moisture or

230   chlorophyll *a*, although a positive trend did exist. ETR was significantly related to both PAR and temperature levels

231   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

232   largely expected (given that light intensity is a factor in calculating electron transport rate), both relationships are

233   consistent in magnitude with the findings of Green and others (1998; 2002) for photobionts.

234   Soil enzyme activity varied significantly by location. POX and LAP (lignin- and protein-degrading

235   enzymes, respectively) both exhibited a negative correlation with soil water content, as activity tended to be highest

236   in the most arid habitats (Table 4). Activity of AG and BG (starch- and cellulose-degrading enzymes, respectively)

237   had an opposite trend with the highest values found in productive soils, while NAG (chitin-degrading) activity

238   exhibited no trend. An index of overall enzyme diversity was calculated using the Shannon-Weiner equation to

239   highlight the relative change in evenness of carbon-acquiring enzyme activity (excluding protein-specific LAP), as

240   described by Tscherko and others (2003). Enzyme diversity had a significant positive relationship with soil moisture

241   ($r^2 = 0.34$; $p < 0.05$) and significant negative relationship with pH ($r^2 = 0.32$; $p < 0.05$). This result is a consequence

242   of high POX activity (as indicated by the relative enzyme activity; Fig. 3) in arid soils, which is gradually replaced

243   by a more even activity of all carbon-acquiring enzymes in productive soils. LAP activity did not correlate with total

244   nitrogen concentrations, or either nitrate-N or ammonium-N (Supplement Data). Multiple regression results suggest

245   soil water content as the driving force behind variation in most factors of biological diversity and activity (Fig 4).

246   **Discussion**

247   Environmental gradients are a key feature of arid environments often chosen for investigation as the

248   inferred mechanism underlying spatial patterns between productivity, for example, and diversity (Noy-Meir 1973).

249   While the diversity of microbial and metazoan communities in Antarctic terrestrial hotspots has been well

250   characterized (Simmons et al. 2009; Zeglin et al. 2011; Niederberger et al. 2015), process based measurements like

251   primary productivity have received less attention. Here we contribute to this understanding of environmental

252   gradients by quantifying the rates of certain key functions that promote and reinforce the habitability of otherwise

253   hyperarid Antarctic soils.

254   PAM fluorometry was used to measure the rate of PSII electron transport rate (ETR), from which was

255   calculated gross primary production (GPP). GPP, organic carbon, and chlorophyll *a* all peaked in the wettest soils

256   that support the densest cryptogam mats. Average GPP was 6.97 μmol $O_2/m^2/s$ in these most productive soils, with a

257   maximum of 17.74 μmol $O_2/m^2/s$ for one location. Assuming a 50% respiratory carbon loss during fixation (i.e. net

258   primary productivity, NPP; Schlesinger 1997) and 60 days of productivity per year (Burkins et al. 2001), this is

259   equivalent to an average NPP rate of ~217 g $C/m^2/y$ with a maximum of 552 g $C/m^2/y$. Considering that some soils

260   in Taylor Valley contain concentrations of organic matter approaching 250 g C/m^2 (Moorhead et al. 2003), mean

261   residence time (pool/flux) of carbon in highly productive zones would equal ~2.2 years. This is substantially lower

262   than the average residence time of decades to centuries estimated for soil organic matter in the broader Taylor

263   Valley landscape (Burkins et al. 2001; Barrett et al. 2005). Organic matter of productive dry valley soils is thus

264   primarily labile photosynthates of recent origin that are rapidly utilized by soil decomposers; this situation is

265   reversed with soil aridity, however, as soil carbon becomes increasingly dominated by recalcitrant substrates of

266   ancient provenance (Burkins 2001).

267   Average GPP for the least productive soils was 0.27 μmol $O_2/m^2/s$. Again assuming that half of gross

268   carbon and oxygen generation from GPP is consumed by respiration, this results in a NPP rate of 0.135 μmol

269    $O_2/m^2/s$ (or 0.135 μmol $CO_2/m^2/s$ of autotrophic respiration). This falls within the range of total soil respiration rates

270   previously described for arid dry valley soils (0.1-0.4 μmol $CO_2/m^2/s$; Burkins et al. 2001; Parsons et al. 2004; Ball

271   et al. 2009) and suggests that autotrophic respiration could constitute a substantial portion of total soil respiration

272   even in arid soils. The consistency of these findings should encourage researchers to couple PAM fluorometry with

273   soil CO_2 flux measurements in future work to attempt distinguishing rates of GPP, NPP, and respiration for producer

274   communities at higher spatial and temporal resolution (Pannewitz et al. 2006). Recent evidence has also suggested

275   that CO_2 efflux measurements from dry mineral soils in this region may be at least partially abiotic in origin

276   (Shanhun et al. 2012; Ball and Virginia 2015), which underscores the limit of CO_2 flux measurements to adequately

277   depict (on its own) biological activity for this region. PAM fluorometry yields independent measures of primary

278   production that can be used to further refine important properties of soil organic matter pools such as residence

279   times.

280   Interestingly, while GPP inferred from PAM fluorometry appears to provide a valuable measure of soil

281   productivity, it did not significantly correlate with chlorophyll levels (Table 3). This suggests that perhaps the better

282   measure of soil productivity may ultimately depend on the temporal scale of inference. Concentrations of soil

283   chlorophyll are thought to represent an integration of producer biomass accrual across days to weeks, from which

284   can be inferred regular moisture availability and stable periods of producer growth. ETR and GPP values, however,

285   provide rapid measures of producer performance under instantaneous light, temperature, and moisture conditions

286   that may not necessarily correlate with chlorophyll concentrations. The sensitivity of producers to rapid

287   environmental change, identification of potential production-limiting stressors, and repeated (non-invasive) long

288   term measures of diel or even seasonal fluctuations in productivity of sample plots may be the best uses of PAM

289   fluorometry. Indeed, previous work has applied PAM measures to reveal the effects of stress and damage to

290   photosystem functioning (Schreiber 2004).

291   Patterns in enzyme activity across the productivity gradient indicate distinct shifts in the nature of detrital

292   pathways as well as organic matter pool complexity. Arid locations exhibited low evenness in an index of carbon-

293   acquiring enzyme diversity, as indicated by the overall dominance of phenol oxidase activity (Fig. 3). This evidence

294   suggests the soil organic matter pool in arid zones may be primarily composed of recalcitrant materials targeted by

295   oxidative enzymes. Although vascular (lignin-bearing) primary producers are absent from this system, recalcitrant

296   compounds may originate from the fatty acids and proteins of decomposing moss and lichen tissue (Beyer et al.

297   1995) deposited during ancient high-stands of a proglacial lake during the Last Glacial Maximum in Taylor Valley

298   (Hall et al. 2000). Such organic matter may be an important energetic source in the more hyperarid soils of this

299   region (Barrett et al. 2006a). In a broader sense the activity of oxidative enzymes worldwide has been found to be

300   greater in drier, more alkaline soils, perhaps a consequence of high mineral surface stability (Zeglin et al. 2009) or

301   higher phenol solubility under such conditions (Sinsabaugh 2010). LAP was also relatively more active in arid rather

302   than mesic locations, potentially indicating greater nitrogen limitation, reduced substrate (protein) availability, or

303   potentially a higher enzyme reactive efficiency at increased pH as suggested by Sinsabaugh and others (2008).

304   Recalcitrant organic substrates that we suspect to predominate in these arid soils, together with low nitrogen

305 availability, likely contribute to the relatively low diversity and enzyme activity of microbial communities found in

306 such habitats.

307   The relative activity of all carbon-acquiring enzymes (i.e. Enz. H') indicated a more even carbon-acquiring

308 enzyme diversity within productive soils (Table 4). From this we infer higher diversity of organic compounds in

309 more productive regions, a logical conclusion considering the presence of greater producer biomass and diversity

310 (Orwin et al. 2006). Increased diversity of organic compounds may therefore be an additional factor behind the

311 greater diversity of organotrophic bacterial communities in productive locations (Grayston et al. 1998). Niche

312 differentiation among microorganisms for various substrates, particularly those that may be decomposed only via

313 specialized enzymatic pathways, may be a mechanism (along with increased resource availability) responsible for

314 increases in microbial diversity. Distinguishing the relative effects of resource quantity and quality remains an

315 important direction for further research to establish important drivers of microbial community diversity.

316   The estimates of primary production we report, even within drier habitats, provide evidence that *in-situ*

317 carbon fixation is occurring widely across the McMurdo Dry Valley landscape with likely effects on subsurface

318 communities and biogeochemical rates. Environmental severity (soil pH, electrical conductivity) and resource

319 availability (soil moisture, organic carbon concentration) vary inversely along a gradient of soil productivity and

320 play important roles in determining biological diversity and activity, although moisture is the primary driver to

321 explain community structure and function (Fig. 4). Changing enzyme activity along this gradient also highlights

322 higher potential organic matter complexity in productive soils, an unforeseen factor that may promote microbial

323 diversity. Our estimates for annual NPP of the most productive dry valley soils, colonized by mixed cyanobacteria

324 and moss mats, indicate yields of ~217 g C/m^2/y, only slightly less than estimates of 250 g C/m^2/y for nearby coastal

325 moss turfs (Pannewitz et al. 2005). We estimate annual NPP for the most arid soils (which dominate the dry valley

326 landscape) to be ~8 g C/m^2/y, and thus an average NPP for Taylor Valley soil productivity would be much lower

327 than the global desert mean of 80 g C/m^2/y (Waide et al. 1999). In spite of these low rates a diverse and active

328 organotrophic community persists here, a testament to the strength of interaction between ecosystem functioning

329 (production, decomposition), environmental conditions (resource quantity/quality), and biotic diversity.

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336   several Virginia Tech collaborators for their contributions towards data acquisition and analysis.

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505   **Table 1**. Description of the five sampling regions from which three locations (each) were chosen to collect samples.

506   Locations within each region were chosen to capture the range of soil primary productivity visually apparent.

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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

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523   **Table 2**. Additional information for enzymatic assays of soils. Standards for the phenol oxidase assay were created

524   by reacting a known mass of L-3,4-dihydroxyphenylalanine substrate with a horseradish peroxidase. 4-MUB = 4-

525   methylumbelliferyl.

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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

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546 **Table 3**. Spearman correlation matrix for soil properties. Electrical conductivity (EC, μS/cm); chlorophyll *a* (Chl*a*,

547 μg/g dry soil); gravimetric moisture (% Moist); soil organic carbon (SOC, mg/kg dry soil); total nitrogen (TN,

548 mg/kg dry soil); microbial biomass carbon (MBC, mg/kg dry soil); TRFLP bacterial diversity (Bact. H'); *a*-

549 glucosidase activity (AG, nmol/g MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr); diversity index of

550 activity for carbon-acquiring enzymes (Enz. H'); electron transport rate (ETR, μmol/m^2/s).

Variable	EC	Chl*a*	% Moist	SOC	TN	MBC	Bact. H'	AG	POX	Enz. H'	ETR
pH	0.61*	-0.36	-0.69**	-0.36	-0.38	-0.55*	0.039	-0.38	0.56*	-0.52*	-0.16
EC		-0.25	-0.62*	-0.39	-0.38	-0.34	-0.26	-0.54*	0.33	-0.59*	-0.63*
Chl*a*			0.80***	0.50	0.55*	0.47	0.57*	0.52*	-0.57*	0.66**	0.48
% Moist				0.40	0.44	0.49	0.57*	0.62*	-0.52*	0.68**	0.50
SOC					0.99***	0.79***	0.13	0.59*	-0.84***	0.61*	0.40
TN						0.80***	0.19	0.61*	-0.86***	0.86***	0.40
MBC							0.00	0.30	-0.89***	0.62*	0.11
Bact. H'								0.57*	-0.03	0.29	0.57
AG									-0.44	0.83***	0.78**
POX										-0.77***	-0.05
Enz. H'											0.63*

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

551 **Table 4.** Average (untransformed) edaphic properties for 15 soil habitats clustered by three productivity zones.

552 Standard error in parentheses except when missing data reduced $n < 3$ (NA). Lowercase letters indicate significant

553 difference by ANOVA ($p < 0.05$). Electrical conductivity (EC, µS/cm); chlorophyll *a* (Chl*a*, µg/g dry soil);

554 gravimetric moisture (% Moist); soil organic carbon (SOC, mg/kg dry soil); total nitrogen (TN, mg/kg dry soil);

555 microbial biomass carbon (MBC, mg/kg dry soil); TRFLP bacterial diversity (Bact. H'); α-glucosidase activity (AG,

556 nmol/g MBC/hr); β-glucosidase activity (BG, nmol/g MBC/hr); N-acetyl-β-glucosaminidase activity (NAG, nmol/g

557 MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr); leucine aminopeptidase activity (LAP, nmol/g MBC/hr);

558 carbon-acquiring enzyme diversity (Enz. H'); electron transport rate (ETR, µmol/m^2/s); gross primary production

559 (GPP, µmol O$_2$/m^2/s).

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Variable	Productivity Zone		
	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)
Chl*a*	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	2.51×10^7a (9.33×10^6)	1.13×10^7a (1.70×10^6)	1.00×10^7a (2.18×10^6)
LAP	1.26×10^6a (2.30×10^5)	9.86×10^5a (1.77×10^5)	8.48×10^5a (1.30×10^5)
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)

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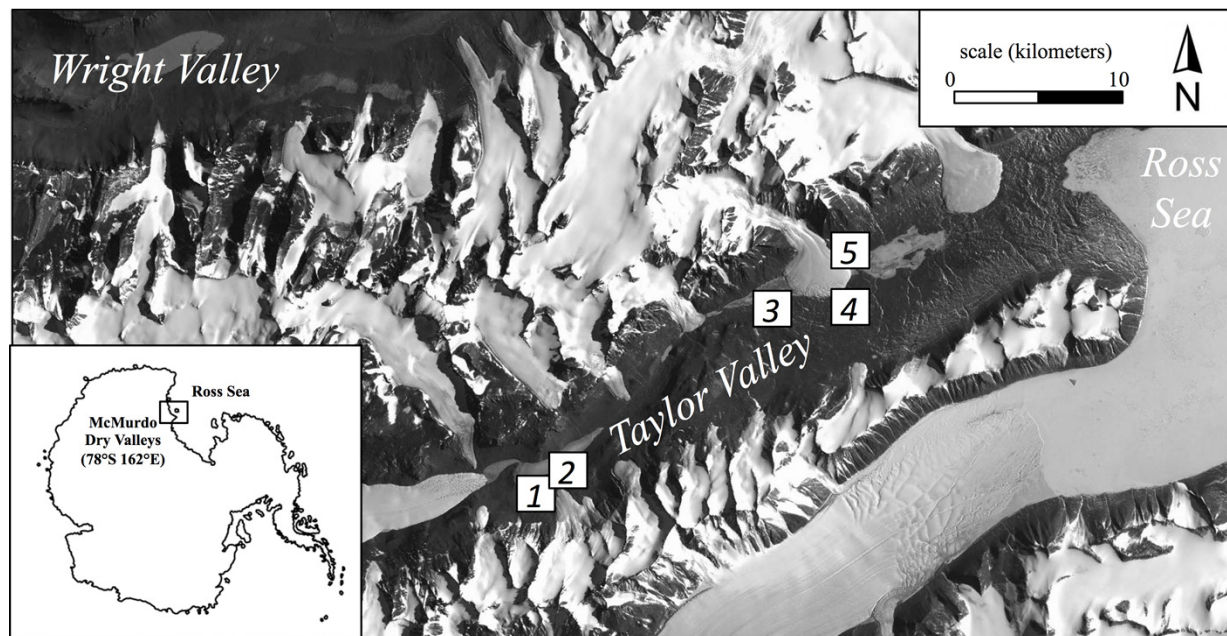
566 **Fig. 1**. Location of the five regional sampling sites in Taylor Valley of the McMurdo Dry Valleys, Antarctica.

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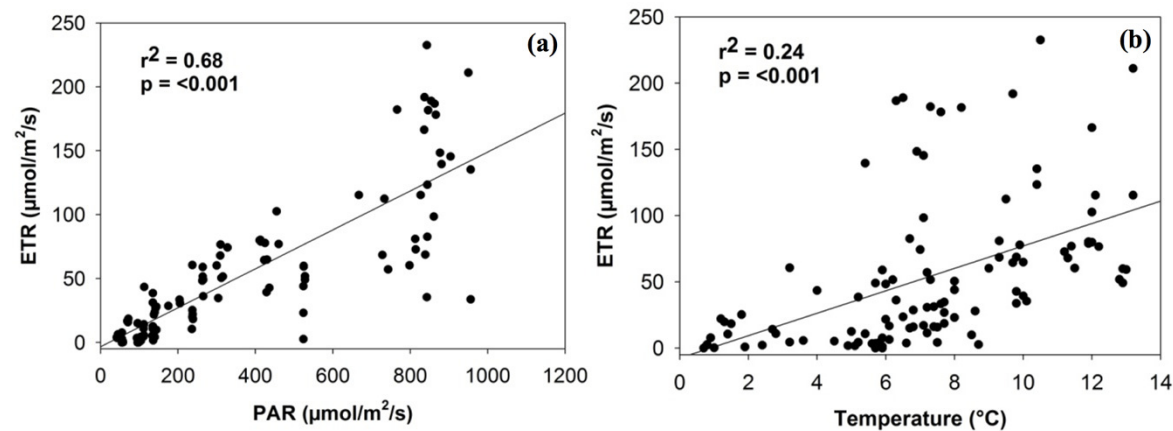
584   **Fig. 2**. Linear relationship between electron transport rate (ETR) and the density of photosynthetically active

585   radiation (PAR) (a) and temperature (b).

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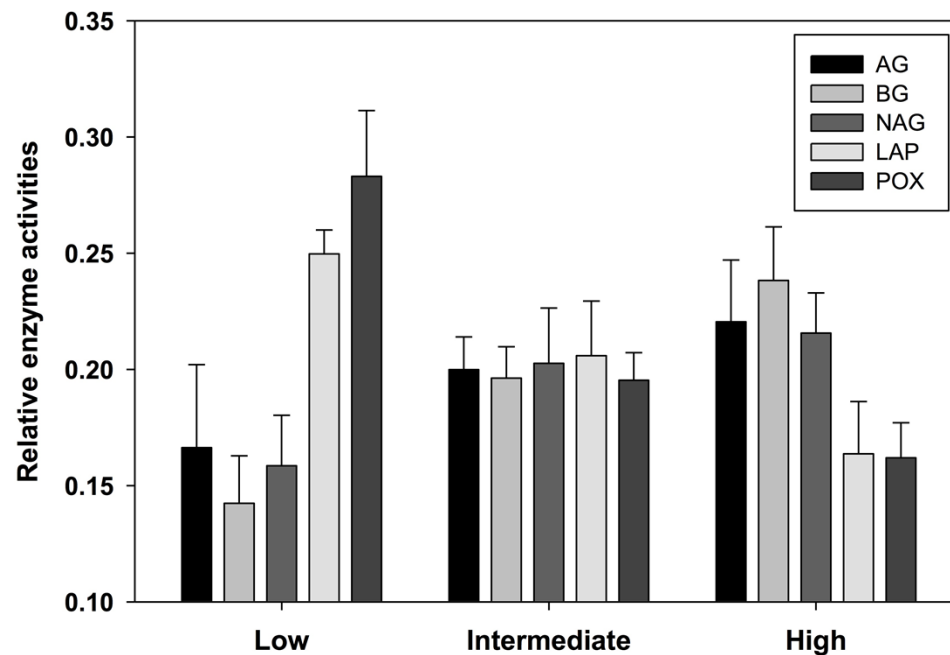
Fig. 3. Relative activity of five standardized ((x-mean)/standard deviation + 3) exoenzymes for sample locations

605 clustered into three productivity classes by soil moisture content. The number of observations are $n = 3$ (Low), $n = 7$

606 (Intermediate), and $n = 5$ (High). α-glucosidase activity (AG, nmol/g MBC/hr); β-glucosidase activity (BG, nmol/g

607 MBC/hr); N-acetyl-β-glucosaminidase activity (NAG, nmol/g MBC/hr); leucine aminopeptidase activity (LAP,

608 nmol/g MBC/hr); phenol oxidase activity (POX, nmol/g MBC/hr).

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Factors	SLR Parameters (r^2)				MLR (R^2)
	% Moist	Chl*a*	pH	EC	
AG	0.36*	0.16	0.14	0.27*	% Moist (0.36)*
BG	0.50**	0.50**	0.21	0.43**	% Moist (0.50)**
POX	0.35*	0.31*	0.26	0.33*	% Moist (0.35)*
LAP	0.14	0.21	0.24	0.09	pH (0.24)
Enz. H'	0.34*	0.29*	0.32*	0.29*	% Moist (0.34)*
Bact. H'	0.34*	0.25	0.01	0.09	% Moist, pH (0.67)**
GPP	0.39*	0.15	0.05	0.38*	% Moist (0.39)*

(a)

(b)

$*p < 0.05; **p < 0.01; ***p < 0.001$
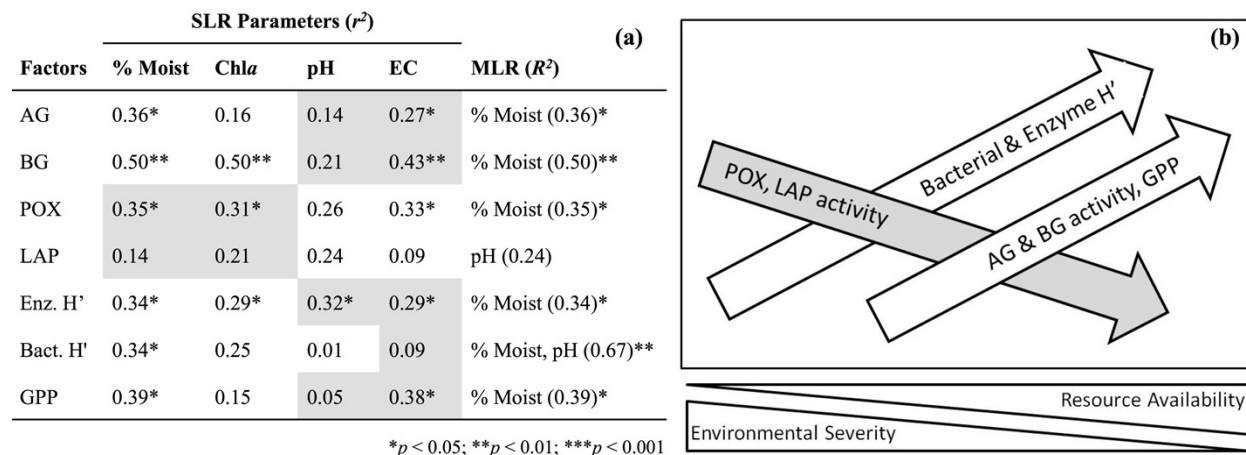
Fig. 4. Simple linear regression (SLR, r^2) results (a) of soil factors against parameters associated with resource availability (e.g. % gravimetric moisture, chlorophyll *a*) and environmental severity (e.g. pH, electrical conductivity). Shaded cells indicate a negative relationship for simple regressions. 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, μS/cm); chlorophyll *a* (Chl*a*, μg/g dry soil) α-glucosidase activity (AG, nmol/g MBC/hr); β-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, μmol $O_2/m^2/s$).