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## Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water

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## Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water

### Abstract

Climate change is expected to affect the high latitudes first and most severely, rendering Antarctica one of the most significant baseline environments for the study of global climate change. The indirect effects of climate warming, including changes to the availability of key environmental resources, such as water and nutrients, are likely to have a greater impact upon continental Antarctic terrestrial ecosystems than the effects of fluctuations in temperature alone. To investigate the likely impacts of a wetter climate on Antarctic terrestrial communities a multi-season, manipulative field experiment was conducted in the floristically important Windmill Islands region of East Antarctica. Four cryptogamic communities (pure bryophyte, moribund bryophyte, crustose and fruticose lichen-dominated) received increased water and/or nutrient additions over two consecutive summer seasons. The increased water approximated an 18% increase in snow melt days (0.2 °C increase in temperature), whilst the nutrient addition of 3.5 g N m<sup>-2</sup> yr<sup>-1</sup> was within the range of soil N in the vicinity. A range of physiological and biochemical measurements were conducted in order to quantify the community response. Whilst an overall increase in productivity in response to water and nutrient additions was observed, productivity appeared to respond more strongly to nutrient additions than to water additions. Pure bryophyte communities, and lichen communities dominated by the genus *Usnea*, showed stronger positive responses to nutrient additions, identifying some communities that may be better able to adapt and prosper under the ameliorating conditions associated with a warmer, wetter future climate. Under such a climate, productivity is overall likely to increase but some cryptogamic communities are likely to thrive more than others. Regeneration of moribund bryophytes appears likely only if a future moisture regime creates consistently moist conditions.

### Keywords

nitrogen, phosphorous, chlorophyll, stable isotopes, <sup>13</sup>C, chlorophyll fluorescence, bryophytes, lichens, ecophysiology, community ecology

### Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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1 **Climate change manipulations show Antarctic flora is more strongly**  
2 **affected by elevated nutrients than water.**

3

4 CLIMATE CHANGE AND ANTARCTIC FLORA

5

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20 **Key words:** nitrogen, phosphorous, chlorophyll, stable isotopes,  $\delta^{13}\text{C}$ , chlorophyll

21 fluorescence, bryophytes, lichens, ecophysiology, community ecology

22

23 **Abbreviations:** Abundance of  $^{13}\text{C}$  stable isotope relative to  $^{12}\text{C}$  ( $\delta^{13}\text{C}$ ), Abundance of  $^{15}\text{N}$

24 stable isotope relative to  $^{14}\text{N}$  ( $\delta^{15}\text{N}$ ), Antarctic Specially Protected Area (ASPA), Dry weight

25 (dw), Electron Transport Rate (ETR), Nitrogen (N), Phosphorous (P), Turf Water Content

26 (TWC).

## 27 **Abstract**

28 Climate change is expected to affect the high latitudes first and most severely, rendering  
29 Antarctica one of the most significant baseline environments for the study of global climate  
30 change. The indirect effects of climate warming, including changes to the availability of key  
31 environmental resources, such as water and nutrients, are likely to have a greater impact upon  
32 continental Antarctic terrestrial ecosystems than the effects of fluctuations in temperature  
33 alone. To investigate the likely impacts of a wetter climate on Antarctic terrestrial  
34 communities a multi-season, manipulative field experiment was conducted in the floristically  
35 important Windmill Islands region of East Antarctica. Four cryptogamic communities (pure  
36 bryophyte, moribund bryophyte, crustose and fruticose lichen-dominated) received increased  
37 water and/or nutrient additions over two consecutive summer seasons. The increased water  
38 approximated an 18% increase in snow melt days (0.2 °C increase in temperature), whilst the  
39 nutrient addition of 3.5 g N m<sup>-2</sup> yr<sup>-1</sup> was within the range of soil N in the vicinity. A range of  
40 physiological and biochemical measurements were conducted in order to quantify the  
41 community response. Whilst an overall increase in productivity in response to water and  
42 nutrient additions was observed, productivity appeared to respond more strongly to nutrient  
43 additions than to water additions. Pure bryophyte communities, and lichen communities  
44 dominated by the genus *Usnea*, showed stronger positive responses to nutrient additions,  
45 identifying some communities that may be better able to adapt and prosper under the  
46 ameliorating conditions associated with a warmer, wetter future climate. Under such a  
47 climate, productivity is overall likely to increase but some cryptogamic communities are  
48 likely to thrive more than others. Regeneration of moribund bryophytes appears likely only if  
49 a future moisture regime creates consistently moist conditions.

## 50 **Introduction**

51 High latitudes are predicted to be the first environments to be affected by the onset of climate  
52 change (IPCC 2001). Climate change in these environments is expected to result not only in  
53 elevated surface temperatures, but also increased precipitation (IPCC 2001; Ye & Mather  
54 1997). Rising temperatures are likely, at least in the short term, to cause additional, indirect  
55 increases in moisture availability in areas receiving meltwater from permeant snow and ice  
56 reserves (Robinson *et al.* 2003). As temperature and moisture are key regulators of soil  
57 microbial activity (Swift *et al.* 1979) the projected increases for these variables are likely to  
58 produce elevated nutrient availability via increased rates of decomposition and nutrient  
59 mineralisation. These indirect effects of climatic change are suggested to be of greater  
60 influence to plant productivity than that of temperature alone (Chapin 1983; Hobbie & Chapin  
61 1998; Delucia *et al.* 2003).

62 The impact of these climate change effects on continental Antarctic terrestrial communities is  
63 not well understood. However, we know from Arctic studies that manipulation of  
64 environmental variables associated with climate change, such as water and/or nutrient  
65 availability, cause significant impacts on communities (Chapin *et al.* 1995; Molau & Alatalo  
66 1998; Press *et al.* 1998a, 1998b; Sandvik & Heegaard 2003). Antarctic terrestrial  
67 communities currently survive some of the most extreme growth conditions on Earth and are  
68 likely to be sensitive to shifts in these conditions.

69 Water and nutrient availability are known to play an important role in the present composition  
70 of Antarctic terrestrial communities, rendering alterations to their availability highly likely to  
71 cause community-level impacts. The low Antarctic temperatures cause most water to be  
72 biologically unavailable, in the forms of snow and ice, creating desert conditions. Water  
73 availability, is therefore thought to be the primary limiting factor for life on this frozen  
74 continent (Kennedy 1993), and has been shown to be the primary determinant of vegetation

75 patterns at both broad- (Broady 1989; Melick *et al.* 1994) and fine-scales (Ryan & Watkins  
76 1989; Selkirk & Seppelt 1987), with bryophytes generally showing greater sensitivity to water  
77 availability than lichens (Leishman & Wild 2001). Patterns of nutrient availability also play a  
78 role in determining vegetation patterns in continental Antarctica (Hovenden & Seppelt 1995;  
79 Ryan & Watkins 1989), particularly with respect to lichens and microalgae (Davey & Rothery  
80 1992; Hovenden & Seppelt 1995; Leishman & Wild 2001).

81 Evidence of past environmental shifts can be observed in the current vegetation structure of  
82 the Windmill Islands region of East Antarctica which is dominated by moribund, lichen-  
83 encrusted bryophytes that are thought to be indicative of a wetter past (Melick & Seppelt  
84 1997). Long-term climatic drying of this region has promoted lichen expansion and the  
85 contraction of bryophytes to only the wettest, low-lying habitats with reliable moisture  
86 supply. Melick & Seppelt (1997) demonstrated, via a growth trial, that this shift in vegetation  
87 structure might be reversible under conditions of increased water availability. In the present  
88 paper, we describe a manipulative field experiment designed to test how increased water and  
89 nutrient availability affects terrestrial communities in continental Antarctica. Four community  
90 types, which occur along an environmental gradient, from bryophyte-dominated habitat at the  
91 edge of a meltlake, to lichen-dominated habitat on the side of a ridge, were investigated.

92 The four experimental communities received water and/or nutrient additions over two  
93 consecutive summer seasons. Our main objectives were to determine if: (1) elevated water  
94 and/or nutrient availability will affect primary production, (2) water additions will have a  
95 greater impact than nutrient additions, (3) the current ambient availability of water and  
96 nutrients differs between community types and (4) some communities respond more strongly  
97 than others to water and/or nutrient additions.

98 As accurate predictions for future water and nutrients are not available for this location our  
99 water and nutrient treatments were chosen to fit within the range of those currently found in

100 the region. Water and nutrient availability to plant communities is currently very patchy  
101 (Beyer & Bölder 1998; Wasley 2004). In this study the water treatment was equivalent to an  
102 increase in snow melt days from 39-46 days (18%) over the summer season. The nutrient  
103 treatment was within the range for current soil nutrients in the vicinity (Beyer & Bölder 1998).

104 The overall aim of the study was to provide an insight into how Antarctic terrestrial  
105 communities are likely to respond to climate change, under a warmer, wetter climate scenario.  
106 We predict that water and nutrient additions will increase plant primary productivity in these  
107 communities. Based on the overall emphasis in the literature, we further predict that plants  
108 will respond more strongly to water-additions than nutrient-additions. The experimentally  
109 manipulated communities are likely to respond differently to water and nutrients and show  
110 variation in the strength and nature of their response to these additions. This experiment is one  
111 of the only multi-season manipulative field experiments that have been conducted in  
112 continental Antarctica (Robinson *et al.* 2003). It therefore provides a particularly important  
113 contribution to our understanding of how plants in this environment are likely to respond to  
114 climate change.

## 115 **Materials and Methods**

### 116 ***Study Area***

117 The Windmill Islands region in East Antarctica is a 40 by 15 km area, consisting of a series of  
118 ice-free islands and peninsulas, topographically characterised by low rounded hills of altitudes  
119 generally less than 100 m. The climate is dry, with the rainfall equivalent of mean annual  
120 snowfall less than 200 mm yr<sup>-1</sup>. Temperatures are cold, with approximate mean monthly  
121 temperatures ranging from 0 °C in the warmest summer months to –15 °C in the winter.  
122 Extremes of temperature range from approximately – 40 to +10 °C. Gale force winds are  
123 common, annually averaging one day in four (Melick & Seppelt 1994).

124 In the past, the region has been completely ice-covered (Hollin & Cameron 1961) and ice  
125 sheet thickness during the Pleistocene is estimated to have been 200 m (Goodwin 1993). The  
126 region became deglaciated during the Holocene, with the south exposed first, 8000 years ago,  
127 and the north a few thousand years later, by 5500 years ago (Goodwin 1993). Since  
128 deglaciation, the land has isostatically uplifted 53 m (Goodwin 1993). As a result of this  
129 uplift, penguin rookeries, which were once close to the sea, have been abandoned as newly  
130 exposed sites closer to the water are occupied. Abandoned penguin colonies are now common  
131 around the 30 m contour, and are frequently colonised by lichens.

132 The Windmill Islands is a botanically important region, supporting some of the most  
133 extensive and best-developed vegetation on continental Antarctica. The entirely cryptogamic  
134 vegetation was first described by Smith (1988), who determined that the region supports at  
135 least 27 species of macrolichens and four bryophytes. Three bipolar lichens dominate the  
136 vegetation *Usnea sphacelata* (Hoffm.) Th. Fr., *Umbilicaria decussata* (Vill.) Zahlbr. and  
137 *Pseudephebe minuscula* (Nyl. Ex Arnold) Brodo & Hawksw., which is typical for continental  
138 Antarctica (Smith 1988).

139 The bryoflora is restricted to low-lying, moist sites, and is composed of three moss species  
140 (*Grimmia antarctici* Card.  $\approx$  *Schistidium antarctici* Card., *Bryum pseudotriquetrum* (Hedw.)  
141 Gaertn., Meyer & Scherb. and *Ceratodon purpureus* (Hedw.) Brid.) and one liverwort  
142 (*Cephaloziella exiliflora* (Tayl.) Steph.). Of these species, the Antarctic endemic *G. antarctici*  
143 is most abundant, while the other two moss species are of widespread cosmopolitan  
144 distributions but locally less abundant. The distribution of these species is thought to be  
145 determined by water availability, as *G. antarctici* is restricted to the wettest sites, *C.*  
146 *purpureus* occupies the driest of sites and *B. pseudotriquetrum* co-occurs with both *G.*  
147 *antarctici* and *C. purpureus* (Selkirk & Seppelt 1987; Wasley 2004). The liverwort, *C.*



148 *exiliflora* has a southern Australasian and scattered Antarctic distribution (Seppelt 1983) and  
149 locally is most commonly found co-occurring with *C. purpureus*.

150 The experimental site was located in the Antarctic Specially Protected Area (ASPAs) 135 on  
151 Bailey Peninsula, approximately 1 km east of Casey Station. Within ASPA 135, the site was  
152 situated on the western edge of a meltlake, close to the ASPA 135 northern boundary, at the  
153 top of a snow slope above Thala valley (66° 16.03' S, 110° 32.53' E). Site aspect was  
154 northeasterly and the site was in the vicinity of an abandoned penguin rookery (Fig. 1). The  
155 site spanned a bryophyte community gradient running up the ridge away from the meltlake;  
156 with pure bryophyte stands at the lake edge, through a moribund bryophyte zone to the point  
157 at which the bryophyte community is predominantly moribund and dominated by crustose  
158 lichen species. This community gradient is thought to occur along a moisture gradient, and is  
159 indicative of a drying trend, along which live bryophyte communities have retreated to low-  
160 lying wet habitats with reliable moisture supply (Melick & Seppelt 1997). Water supply for  
161 these communities is mainly from melting of overlying snow, which transiently saturates the  
162 plants. However, the moss community on the lake edge remains waterlogged for most of the  
163 growing season.

#### 164 **Experimental design**

165 Within the experimental site, four community types were identified based on the percentage  
166 cover of four key community components: healthy bryophytes, moribund bryophytes,  
167 crustose lichens and macrolichens of the genus *Usnea* (details of community composition are  
168 given in Fig. 1). The Bryophyte and Crustose communities correspond to Group 1 and 2.3,  
169 respectively, in Melick & Seppelt (1997). The Moribund community is an intermediate  
170 community. The *Usnea* community corresponds with Group 2.5 (Transitional, Foliose lichen-  
171 dominated, *Usnea*; Melick and Seppelt 1997). This latter community is considered to be the

172 earliest indicator of the presence of extant bryophyte communities, which thrived when  
173 conditions were moister.

174 The four communities occurred along a gentle slope, with an easterly aspect, between the  
175 meltlake edge and the side of a small ridge. The Bryophyte community occurred closest to the  
176 meltlake, and the other three communities were positioned with increasing distance from the  
177 meltlake edge, in the order of: Moribund community, Crustose community and, furthest from  
178 the meltlake, the *Usnea* community, which was closest to the ridge (Fig. 1).

179 Within each community, 32 equivalent quadrats (25 x 25 cm) were randomly assigned one of  
180 the following four treatments: (1) no-treatment (NT-), (2) water only (W-), (3) nutrient only  
181 (N-), or (4) water & nutrient (WN-). The two water addition treatments (W- and WN-) had  
182 500 ml of meltlake water applied approximately every two days across the 1998/99 and  
183 1999/00 summer seasons (December - February). To avoid beading of the applied water off  
184 the vegetation surfaces, and therefore maximise the effectiveness of the water additions, each  
185 quadrat was first pre-soaked using a fine, firm, even spray of water from a pressurised spray  
186 bottle. The remaining treatment water was then slowly and evenly poured over the area of the  
187 quadrat. The water treatment was intended to alleviate water limitation by saturating the turf  
188 at each application. The 500 mL additions were excess to that absorbed and simulated an  
189 increase in snow melt days from 39 to 46, equivalent to a 0.2 °C increase in temperature over  
190 the summer months (Dunn & Robinson *pers. comm.*). Since all three moss study species grow  
191 in areas which become periodically saturated this was a realistic treatment assuming either  
192 increased snowfall or increased melt. The water was taken from the meltlake adjacent to the  
193 site; as this is a natural water source of the bryophyte communities at the height of the  
194 summer melt.

195 Quadrats receiving nutrient additions (N- and WN-) had 10 g of slow release fertiliser beads  
196 (Osmocote, Scotts Australia Pty. Ltd., Castle Hill, NSW, Australia) applied at the start of the

197 treatment period (15/12/98). The Osmocote was composed of 18% nitrogen (7.5% as nitrate,  
198 10.5% as ammonium), 4.8% phosphorous (4.3% water soluble, 0.5% citrate soluble), 9.1%  
199 potassium (as potassium sulphate), 4.0% sulphur (as sulphate) and 1.0% calcium phosphate  
200 and calcium sulphate, with a 9.1% organic resin coating. These additions constituted  
201 approximately  $3.5 \text{ g N m}^{-2} \text{ yr}^{-1}$  and  $1 \text{ g P m}^{-2} \text{ yr}^{-1}$ , which is comparable to additions used in  
202 Arctic climate change simulation studies (Chapin *et al.* 1995; Molau & Alatalo 1998), and  
203 low relative to the N storage of Windmill Islands' soils ( $21\text{-}736 \text{ g N m}^{-2}$ ; Beyer & Bölter  
204 1998). This type of fertiliser treatment was chosen to achieve a slow release of nutrients over  
205 the duration of the study period, avoiding both nutrient "spikes" and the need to reapply  
206 nutrients with multiple applications. Beads were inserted into the bryophyte turf and/or lichen  
207 crust with tweezers to ensure nutrient additions remained within relevant treatment quadrats.  
208 Empty beads were recovered at the end of the study period, indicating that the fertilizer  
209 treatments had remained in place.

### 210 ***Primary productivity surrogates***

211 In other high-latitude ecosystems, ecological measures of community change (such as,  
212 biomass and species cover) have been successfully used to monitor response to environmental  
213 manipulations (Press *et al.* 1998b; Robinson *et al.* 1998). The characteristically slow growth  
214 rates that occur in continental Antarctica (Green 1985), however, limit studies of this nature to  
215 utilising physiological methodologies. Instead of using direct measures of growth, such as  
216 biomass, a variety of physiological measurements were used as surrogates for primary  
217 productivity and the growth environment.

218 Chlorophyll fluorescence, chlorophyll and plant nutrient content and stable isotope ratios  
219 were measured for representative vegetation within each community type. Samples from the  
220 Bryophyte, Moribund and Crustose communities consisted of well-developed bryophyte turf,  
221 increasingly moribund and encrusted with crustose lichens in the Crustose community.

222 Samples from the *Usnea* community consisted of only a thin bryophyte crust and were  
223 dominated by lichens, predominantly from the genus *Usnea*.

#### 224 **Field measurement of chlorophyll fluorescence**

225 Chlorophyll *a* fluorescence is particularly useful for measuring photosynthesis in Antarctic  
226 cryptogams, since their small size makes gas exchange measurements difficult (Green *et al.*  
227 1998; Lovelock *et al.* 1995a, 1995b) and such non-destructive methods are ideal where plant  
228 conservation is a major concern. Although electron transport rate (ETR) is not a direct  
229 measure of photosynthetic gas exchange, simultaneous fluorescence and gas exchange  
230 measurements have shown that fluorescence ETR measurements correlate directly with CO<sub>2</sub>  
231 gas exchange in the moss species *Bryum argenteum* (Schroeter *et al* 1995) and *Ceratodon*  
232 *purpureus* (J. Wasley, *unpublished data*).

233 Electron transport rates were measured using chlorophyll fluorescence during the main  
234 growing season (14-15/2/00). Replicate measurements were taken under consistent light  
235 conditions, between 2 & 4 pm, within randomly selected quadrats (n=6) from each  
236 community and treatment. Measurements were performed using a MINI-PAM equipped with  
237 a micro leaf clip (Walz, Effeltrich, Germany). ETR was calculated using the equation:  $ETR =$   
238  $\phi_{PSII} * PAR * 0.5 * 0.84$ , as described by Maxwell & Johnson (2000). ETR was used in  
239 preference to measures such as the ratio of variable to maximal fluorescence (Fv/Fm), which  
240 requires a dark adaptation period. Dark adaptation of plant material was found to be  
241 unsuitable in this environment, since plant tissue temperature declined significantly as soon as  
242 solar radiation was interrupted.

#### 243 **Laboratory analysis of chlorophyll, nutrients and stable isotopes**

244 At the end of the treatment period (3-8/3/00), representative community samples were  
245 collected for pigment and nutrient analyses. Seven replicate quadrats were sampled over a 5-  
246 day period from each of the sixteen treatment and community groups. Samples of

247 approximately 4 cm<sup>2</sup> were collected from the centre of each quadrat, in subsets of 16, each  
248 subset including one replicate from each community and treatment type.

249 Each sample was divided into three; approximately 1 cm<sup>2</sup> area comprised the chlorophyll  
250 pigment and turf water content (TWC) samples for which the surface portion (top 2-3 mm)  
251 was reserved for chlorophyll pigment analyses and the base was used to estimate TWC. Of  
252 the remaining larger portion (approximately 3 cm<sup>2</sup>), the top 1 cm was used to determine plant  
253 nutrient contents (N and P). For each sample, total chlorophyll, TWC, nutrient (N and P) and  
254 stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) signatures were determined, as described below.

255 Samples for chlorophyll determinations were frozen in liquid nitrogen, transported to  
256 Australia and stored at -80 °C until analysis. Pigments were extracted into 80% acetone from  
257 approx 0.02-0.20 g of plant samples and chlorophyll analysed using the method of Porra *et al.*  
258 (1989).

259 The availability of water in the growth environment was determined for samples of bryophyte  
260 turf that were collected from the field in airtight vials. Using an analytical balance, fresh  
261 weight was determined immediately upon return to the laboratory. Dry weights were  
262 determined after oven drying at approximately 70 °C, till constant weight. The turf water  
263 content (TWC) of each moss sample at each time period was determined as described in  
264 Robinson *et al.* (2000, 2005).

265 Prior to determination of nitrogen, phosphorus,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , plant material was oven dried,  
266 as described for TWC and ground to a fine powder (0.2 mm particles) in a ball mill (Retsch  
267 MM2, Vienna, Austria). Aliquots of 1 to 2 mg of each sample were analysed by continuous-  
268 flow gas isotope ratio mass spectrometry after Hietz *et al.* (1999). The elemental analyzer (EA  
269 1110, CE Instruments, Milan, Italy) was interfaced via a ConFlo II device (Finnigan MAT,  
270 Bremen, Germany) to the gas isotope ratio mass spectrometer (DeltaPLUS, Finnigan MAT).

271 Total phosphorous was determined in duplicate for each sample by HNO<sub>3</sub>-H<sub>2</sub>SO<sub>4</sub> digestion,  
272 followed by stannous chloride colorimetry determined at 690 nm (Clesceri *et al.* 1998;  
273 Spectronic 21D, Spectronic Instruments, Leeds, UK).

274 In the *Usnea* community, it was difficult to collect pure vegetation samples that were free of  
275 soil contamination, as bryophytes occurred in this community only as a thin moribund crust,  
276 rather than a well-developed turf. To calculate nutrient contents on a dry weight basis, ash  
277 weights of samples were determined and weight % N and P corrected as described in Wasley  
278 (2004).

### 279 **Statistical Analysis**

280 For each of the biological parameters measured, a two-way ANOVA was conducted, testing  
281 means for community differences, treatment effects and treatment x community interactions.  
282 Transformations of the data were required in some cases to ensure an acceptable level of  
283 normality and homoscedacity (see Table 1). Where the treatment x community interaction  
284 was significant, *post hoc* pairwise (Student's t) tests were conducted for all ecologically  
285 relevant pairs of means (i.e. within both treatment and community groups) in conjunction  
286 with the Bonferroni procedure (Rice 1989). As the Bonferroni procedure reduces the alpha  
287 level, and in turn the chance of identifying significant pairs, it is argued that the Bonferroni  
288 procedure can sometimes cause biologically important difference to be overlooked (Moran  
289 2003). For this reason, any additional pairs of means that are significant at  $\alpha = 0.05$  are  
290 reported. The results of these pairs must be interpreted with caution, but are worth noting, as  
291 they are potentially biologically significant. Statistical tests were conducted using JMP  
292 software (SAS Inc., Cary, NC, USA).

293

## 294 **Results**

### 295 ***Photosynthetic efficiency***

296 Photosynthetic ETR was similar in the control group (NT-) across the communities, and all  
297 communities showed a positive response to the water and/or nutrient additions (Fig. 2A).  
298 Several notable community differences were found, as the strength and nature of the treatment  
299 response differed across communities (treatment x community interaction:  $P = 0.0003$ ; Table  
300 1). The treatment response was weak (not significant) in the Moribund and *Usnea*  
301 communities, and strongest in the Crustose and Bryophyte communities. The strongest  
302 response to treatments was found in the Crustose community, where ETRs in all treatment  
303 groups were greater than 4-fold higher than the untreated control ( $P < 0.002$ ). This community  
304 responded more strongly to the addition of water than nutrients, as the two water-treatments  
305 (W- and WN-) had significantly higher ETRs than the nutrient-only treatment ( $P < 0.002$  and  
306  $0.05$ , respectively). Conversely, the Bryophyte community, which also showed a significant  
307 treatment response, responded most strongly to nutrient additions, with ETRs highest in the  
308 two nutrient treatments where rates were more than 2-fold higher than the untreated control  
309 (N-  $P < 0.05$ , WN-  $P < 0.002$ ). In this community the effect of water alone was not significant  
310 ( $P > 0.05$ ). Although the moribund community response was not significant, all treatments  
311 resulted in 2-fold higher ETRs than untreated samples.

### 312 ***Total chlorophyll***

313 Nutrient additions had a positive effect on concentration of total chlorophyll, particularly in  
314 the Bryophyte and Crustose communities (treatment effect:  $P < 0.0001$ ; Table 1) where total  
315 chlorophyll concentrations were 2- to 3-fold greater in the two nutrient-treatment groups (N-  
316 and WN-), compared to the corresponding non-nutrient treated groups (NT- and W-;  
317 community effect,  $P < 0.0001$ ; Table 1; Fig. 2B). The Moribund and *Usnea* communities  
318 showed a relatively weak treatment response. Concentration of total chlorophyll also differed

319 between the communities, with Crustose having the highest and Moribund the lowest overall  
320 concentrations ( $P < 0.008$ ). Chlorophyll a/b ratios, which ranged from approximately 1.5 to  
321 3.0, showed significant differences between communities, but there was no effect of  
322 treatment. Ratios were highest in the lichen-dominated Crustose and *Usnea* communities  
323 ( $P < 0.008$ ).

## 324 **Water, nutrient and stable isotope composition**

### 325 **Turf water content**

326 Turf water content (TWC; g H<sub>2</sub>O g<sup>-1</sup> dry wt.) ranged from just less than 1 to slightly over 2 g  
327 H<sub>2</sub>O g<sup>-1</sup> dry wt. (Fig. 3A). Water and/or nutrient additions had no significant effect on TWC,  
328 but there was significant variation between the communities (Table 1), with the Crustose and  
329 Bryophyte communities having higher TWCs than the relatively dry Moribund and *Usnea*  
330 communities ( $P < 0.008$  and 0.05, respectively).

### 331 **Nutrients**

332 Nutrient additions (N-) enhanced weight %N in all communities except the Moribund  
333 community (overall model:  $P < 0.0001$ ; treatment x community interaction:  $P = 0.0340$ ; Table  
334 1; Fig. 3B). In all three communities showing this response, the nutrient-only additions (N-)  
335 produced %N levels that were significantly higher than both the non-nutrient treated groups  
336 (NT- and W-,  $P < 0.002$  and 0.05, respectively). In the Crustose community, nutrient only  
337 additions also elevated %N significantly more than the combined water and nutrient additions  
338 ( $P < 0.002$ ). The *Usnea* community was the only community in which the combined water and  
339 nutrient treatment (WN-) enhanced %N significantly over levels in untreated control samples  
340 (NT-,  $P < 0.05$ ).

341 Elevated water and/or nutrient availability did not significantly alter %P, but significant  
342 community differences for this variable were identified (Table 1). Percent P showed a strong  
343 community gradient (community effect:  $P < 0.0001$ ; Table 1), with a greater than 20-fold



344 increase from the Bryophyte to the *Usnea* community ( $P<0.008$ ; Fig 3C). Percent N was also  
345 lowest in the Bryophyte community ( $P<0.002$ ), and generally highest in the Crustose  
346 community, where control levels (NT-) were significantly higher than all communities except  
347 Moribund ( $P<0.002$ ).

### 348 **Stable Isotopes**

349 Water and/or nutrient additions did not significantly alter stable isotopic signatures for  $^{15}\text{N}$  or  
350  $^{13}\text{C}$  (Table 1), indicating the fertilizer did not significantly affect  $\delta^{15}\text{N}$ , nor did the watering  
351 regime significantly alter  $\delta^{13}\text{C}$  (Fig. 3D). There was, however, significant community  
352 variation in stable isotopic signatures (community effect:  $P = <0.0001$ ; Table 1). Variation  
353 between communities was primarily due to distinctions in  $\delta^{13}\text{C}$ , rather than  $\delta^{15}\text{N}$  (data not  
354 shown). The most notable community distinction found for  $\delta^{15}\text{N}$  were the Crustose  
355 community values, which were significantly more positive ( $13.6\pm 1.9\text{‰}$ ,  $n=6$  to  $17.4\pm 1.9\text{‰}$ ,  
356  $n=5$ ) than the other three communities ( $6.2\pm 0.9\text{‰}$  to  $11.7\pm 2.4\text{‰}$ ,  $n=7$ ;  $P<0.008$ ). Much  
357 stronger community differences occurred in  $\delta^{13}\text{C}$  signatures, for which each community was  
358 significantly different to the others ( $P<0.008$ ), with values highest (least negative) in the  
359 Bryophyte community and lowest (most negative) in the *Usnea* community (Fig. 3D).

### 360 **Discussion**

361 On this desert continent, water is considered to be the most limiting environmental parameter  
362 to plant life (Robinson *et al.* 2003, Wasley *et al.* 2006), more so even than the direct  
363 limitations associated with the low temperatures that dominate this ecosystem. It was  
364 therefore expected, that increased water availability, would be most influential and that the  
365 addition of nutrients, which are generally not considered limiting (Robinson *et al.* 2003),  
366 would have a secondary, but possibly synergistic, effect. This study shows a positive response  
367 to increased water availability, but surprisingly, a strong positive response to nutrient  
368 additions was also found. Background availability of the two manipulated environmental

369 variables varied across the site, producing differences in availability of these resources  
370 between the communities. Thus natural variation in resource availability, likely influenced the  
371 differences in treatment-response that were found across the communities.

372 The water and nutrient treatments used in this study were designed to alleviate water and/or  
373 nutrient limitations, with quantities applied within the range currently found in the region.

374 The rationale for this approach is two-fold, firstly to investigate biological response under  
375 non-limiting conditions and secondly due to the difficulties associated with predicting future  
376 water and nutrient availability and patchiness. In the Antarctic environment, precipitation  
377 levels are difficult to measure due to interference with blowing snow and ice across the  
378 landscape. This renders estimates of present water availability to plant communities difficult  
379 and makes modelling of future availability unreliable for application to this type of study.

380 Similarly, the increase in future nutrient availability will remain difficult to quantify until  
381 more certainty is developed regarding future temperature conditions and water availability.

382 However, global warming is likely to increase thawing depth, releasing N and P from the  
383 permafrost (Beyer & Bølter 1998). Nutrient inputs from bird sources are important to present  
384 vegetation patterns (isotopic data presented here, Leishman & Wild 2001; Ryan & Watkins  
385 1989) and changes to this nutrient source will also impact on future nutrient availability.

386 This discussion focuses on three of the main findings of this study. Firstly, we discuss  
387 gradients in water and nutrient availability across the site and their relationship to plant  
388 community types. Secondly, community differences in treatment-response are discussed,  
389 which support the hypothesis that some communities would respond more strongly than  
390 others to water and/or nutrient additions. Finally, we discuss how this study offers support for  
391 the hypotheses that elevated water and/or nutrient availability affects primary production  
392 surrogates, but does not support the hypothesis that water additions will have a greater impact  
393 than nutrient additions.

## 394 **Environmental gradients**

395 The ambient availability of water and nutrients differed between the communities. These  
396 differences were largely determined by two opposing environmental gradients across the site,  
397 one a gradient in water availability, the other a gradient in nutrient availability (Wasley 2004).

## 398 **Water availability**

399 As the site was situated on the edge of a meltlake, a moisture gradient occurred across the site,  
400 with the Bryophyte community occupying the lowest-lying, wettest habitat and the *Usnea*  
401 community the highest and driest (Fig. 1). Community patterns of  $\delta^{13}\text{C}$  support the presence  
402 of this gradient in water availability. More positive  $\delta^{13}\text{C}$  values are indicative of less  
403 photosynthetic isotopic fractionation, resulting from diffusional limitations reducing the  
404 concentration of  $\text{CO}_2$  reaching the site of RUBISCO. In higher plants this diffusional  
405 fractionation relates to stomatal opening. However in cryptogams it likely reflects the degree  
406 to which plants are submerged in water and the consequent diffusional limitations (Bottger *et*  
407 *al.* 1993; Proctor *et al.* 1992; Rice & Giles 1996). Cryptogams subject to submergence are  
408 expected to show elevated (less negative)  $\delta^{13}\text{C}$  signatures, as has been shown in *Sphagnum*  
409 *trinitense* (Proctor *et al.* 1992). The relatively high  $\delta^{13}\text{C}$  found for the Bryophyte community  
410 in this study (control:  $-22.7 \pm 0.1\%$ ,  $n=6$ ) represents a cumulative signature, reflecting a  
411 tendency for periodic submergence during the summer melt. The  $\delta^{13}\text{C}$  community patterns  
412 therefore likely reflect a submergence gradient, and field observations strongly support the  
413 occurrence of periodic submergence in the Bryophyte community during the growing season.

414 Values for  $\delta^{13}\text{C}$  provided stronger support for the presence of a moisture gradient occurring  
415 across the site than did turf water contents. It is likely, however, that for a single measurement  
416 interval  $\delta^{13}\text{C}$  is a better integrator of plant moisture availability over the season, as it provides  
417 cumulative evidence of submergence. Turf water content is an instantaneous measurement  
418 and does not necessarily reflect water availability for the majority of the growth season. We

419 suggest that the anomaly between TWC and  $\delta^{13}\text{C}$  is not due to the lack of change in water  
420 availability over the site, but instead reflects the timing of sample collection and site  
421 topography. Samples were collected late in the season, by which time the level of water in the  
422 meltlake had dropped and the water had frozen; leaving the Bryophyte community relatively  
423 dry and at a seasonally low level. Moreover, sample collection occurred after snowfall, and  
424 snow accumulation across the site therefore resulted in elevated moisture in the other  
425 communities at that time. These factors, combined, explain the lack of evidence for a moisture  
426 gradient presented in the TWC data.

427 Site topography is likely to have contributed toward the relatively high moisture contents  
428 found in the Crustose community and  $\delta^{13}\text{C}$  data suggest that this represents the second most  
429 submerged community (Fig. 3D). This community was situated on a relatively flat, terraced  
430 section in the middle of the site (Fig. 1), causing the snowfall to accumulate on this  
431 community. We therefore suggest, that the turf water content data was collected at a time  
432 when the Bryophyte community was drier than usual and the Crustose community wetter than  
433 usual, and is not necessarily representative of the water contents of these communities for the  
434 majority of the growing season. Field observations,  $\delta^{13}\text{C}$  values and data from adjacent sites  
435 supporting comparable communities provide strong evidence that a submergence gradient is  
436 present across this site for the majority of the growth season (Wasley *et al.* 2006).

### 437 **Nutrient availability**

438 Fractionation of nitrogen isotopes provides information about plant nitrogen sources  
439 (BassiriRad *et al.* 2003; Bragazza *et al.* 2005). Antarctic plants commonly have high  $\delta^{15}\text{N}$ ,  
440 due to utilisation of nutrients derived from marine animal sources such as penguins (Cocks *et*  
441 *al.* 1998a, 1998b; Robinson 2001). Although there are few present day inputs at the study site,  
442 an abandoned penguin rookery was located at the top of the low rocky ridge above the site.  
443 Such abandoned rookeries are known to provide a significant nutrient source to plants in

444 Antarctic terrestrial communities (Hovenden & Seppelt 1995; Tatur & Myrcha 1989).  
445 Nutrients deposited when these rookeries were occupied, approximately 5000 years ago  
446 (Goodwin 1993), undergo further  $^{15}\text{N}$  fractionation as the guano passes through additional  
447 tropic levels associated with decomposition. Plants utilising this ancient nitrogen source are  
448 expected to have exceptionally high  $\delta^{15}\text{N}$  values higher than +14.6‰, the value for fresh  
449 penguin guano (Robinson 2001). Lower  $\delta^{15}\text{N}$  values indicate plants are receiving a higher  
450 proportion of volatilised wind-born  $\text{NH}_3$  from present-day rookeries (Robinson 2001) and/or  
451 cyanobacterial N fixation. The high  $\delta^{15}\text{N}$  values found in plant material in this study indicate  
452 that the nutrient source for this community is likely to be the nearby abandoned penguin  
453 rookery. Soil in the vicinity of the site also had high  $\delta^{15}\text{N}$  ( $23.84 \pm 1.18\text{‰}$ ,  $n=6$ ; Wasley 2004).  
454 We suggest this rookery provides a significant nutrient-source for the site and underlies the  
455 gradient in nutrient availability observed across the site.

456 Plant nutrient content was highest in communities closest to the ridge and declined with  
457 distance from the rookery, confirming the rookery as the major nutrient-source for the site  
458 (Fig. 3B&C). This pattern was particularly strong for phosphorous. Substratum nutrient  
459 concentrations in the Hovenden & Seppelt (1995) abandoned rookery site match the patterns  
460 found in the present study; phosphorous declined 15-fold within 25 m from the rookery, while  
461 nitrogen showed a less sharp decline, of less than 2-fold, over the same distance.

462 Site hydrology is also likely to interact with plant nutrient contents. The nearby lake drains  
463 into a stream that flows out of the site. Snow melt moving down the slope, from the  
464 abandoned rookery on the ridge, to the lake is likely to be a source of nutrients, but the wetter  
465 community at the edge of the lake (i.e. Bryophyte community) is likely to be heavily leached  
466 as nutrients flow out of the catchment. The terrace upon which the Crustose community is  
467 positioned might act to sequester nutrients for a longer period than on the steeper slopes  
468 and/or the periodically submerged lakeside positions.

469 **Community response to water and nutrient additions**

470 Differences in treatment-response were found for the four experimentally manipulated  
471 communities, supporting the hypothesis that some communities would respond more strongly  
472 than others to water and/or nutrient additions. Overall, the Bryophyte and Crustose  
473 communities showed a strong treatment-response, while the Moribund and *Usnea*  
474 communities responded weakly.

475 The Bryophyte community responded most strongly to nutrient additions in both primary  
476 productivity surrogates. The Crustose community similarly showed a strong increase in total  
477 chlorophyll in response to nutrient additions but in contrast, ETR responded more strongly to  
478 water additions. Some of these community differences in treatment-response were likely to be  
479 related to the resource availability gradients that were observed across the site. The Bryophyte  
480 community, for example, in which water contents are usually highest, responded most  
481 strongly to nutrients. While the Crustose community, in which water availability is estimated  
482 to be relatively low for much of the growing season, showed a response to both treatments.

483 Although not significant, there are indications that the treatments increased productivity in the  
484 *Usnea* and Moribund communities. Such a limited response was particularly unexpected for  
485 the Moribund community. This community is thought to have formed in response to a drying  
486 trend, and it was predicted that lichen encrusted moribund moss, which characterises this  
487 community, may have shown regeneration potential in response to water additions, as this has  
488 been shown to occur under controlled growth conditions (Melick & Seppelt 1997). It is  
489 possible that the water treatment was not sufficient for moss regeneration, but it may also be  
490 that the encrusting lichen species were responsible for this lack of recovery through  
491 allelopathy. Species of the genus *Buellia* are commonly found encrusting moss in this study  
492 area and it has been suggested that this species exhibits allelopathic characteristics (Melick &  
493 Seppelt 1997). It is therefore possible, that the allelopathic effects of lichens or the action of

494 antagonistic fungi (Melick & Seppelt 1994) were responsible for the limited response of this  
495 community. This finding is particularly important since it suggests that changes to water  
496 availability alone may not be sufficient to reverse the trend of drying climate producing  
497 moribund moss.

498 Live bryophyte material is present in the Crustose and Moribund communities (Wasley 2004),  
499 it is likely, however, that only conditions of consistent soaking would allow them to  
500 regenerate. If this is the case, regeneration will only be likely under a future climate that  
501 produces increased frequency and intensity of water availability. Otherwise, it is likely that  
502 crustose lichens will continue to expand in distribution, encrusting bryophyte turfs.

### 503 ***Impacts on primary productivity surrogates***

504 Although the hypothesis that elevated water and/or nutrient availability will affect primary  
505 productivity surrogates is supported, the hypothesis that water additions will have a greater  
506 impact than nutrient additions is not. The impacts of water and/or nutrient additions are  
507 summarised below.

### 508 **Response to water additions**

509 The strongest response to water additions was found in the Crustose community, where  
510 photosynthetic rates increased more than 7-fold in response to the watering treatment (Fig.  
511 2A). Turf water contents suggest that, at the time of sample collection, water availability was  
512 relatively high in this community (Fig. 3A). Field observations and  $\delta^{13}\text{C}$  values suggest,  
513 however, that this community was drier than the Bryophyte community, for the majority of  
514 the growth season, explaining why the response to water-treatment was less pronounced in the  
515 Bryophyte community. Although the Crustose community showed a nutrient response (see  
516 below) the water response was stronger. Weaker than expected responses to water additions  
517 have also been observed in temperate grassland bryophyte communities (Bates *et al.* 2005).

518 **Response to nutrient additions**

519 Despite the general suggestion that nutrients are non-limiting to Antarctic plant physiological  
520 processes (Robinson *et al.* 2003), this study found strong responses to nutrient additions,  
521 supported by a 3-fold increase in total chlorophyll concentration and 4-fold increase in ETR  
522 in the Bryophyte and Crustose communities, respectively.

523 Plant nitrogen increased significantly in response to the nutrient-only additions in all but the  
524 Moribund community, with the most striking increases occurring in the *Usnea* community  
525 where %N almost doubled (Fig. 3B). These nutrient increases indicate sufficient natural  
526 moisture availability within most communities for nutrient uptake, and that the nutrient  
527 treatments were effective. With increased replication it seems likely that the nutrient  
528 treatments would deliver significantly higher productivity parameters in all communities,  
529 including *Usnea* and Moribund.

530 Increasing ETR, in response to the water and nutrient additions, suggests that the plants are  
531 limited by these environmental factors and have the ability to respond by increasing  
532 photosynthesis. If increases in the concentration of N or chlorophyll had been the only  
533 response this might have indicated the plants simply absorb the nutrients and sequester them,  
534 but are in fact limited by other factors in terms of photosynthetic rate. These results support  
535 increased photosynthetic productivity as a result of nutrient additions. Further long-term  
536 studies would be required to show if growth was positively affected by nutrients.

537 It has previously been suggested that sufficient nitrogen is available in precipitation  
538 (Greenfield 1992) but the nutrient response observed in this study suggests these communities  
539 may be experiencing nutrient-limitations. Although soil nutrients are quite high in this region  
540 (Beyer & Bölter 1998), they may not be readily available to cryptogams which lack roots.  
541 Other examples of nutrient-limitation in Antarctic terrestrial communities have been reported,  
542 including nutrient-limited growth of lichens situated away from bird colonies (Ryan &



543 Watkins 1989), nitrate limitation of microalgae in fellfield soils in the maritime Antarctic  
544 (Davey & Rothery 1992; Arnold *et al.* 2003) and nutrient-limited bryophyte carbon  
545 assimilation in the sub-Antarctic (Smith 1993). In milder and subarctic sites, climate warming  
546 is predicted to reduce bryophyte and lichen cover as a result of poor nutrient competitiveness  
547 against vascular plants (Cornelissen *et al.* 2001; Epstein *et al.* 2004; Wahren *et al.* 2005)  
548 whereas in the high arctic bryophytes also respond positively to nutrient additions (Robinson  
549 *et al.* 1998; van Wijk *et al.* 2004). This study concurs with these latter studies suggesting that  
550 nutrient-limitations may be widespread in both Antarctic and high Arctic systems (Jonasson  
551 1992; Robinson *et al.* 2004; van Wijk *et al.* 2004). This study does not allow us to determine  
552 which nutrients are limiting, and it is possible that nitrogen, phosphorus, or a combination of  
553 nutrients, are responsible for these strong nutrient treatment responses.

#### 554 **Synergistic effects**

555 Some evidence that combined water and nutrient additions had a synergistic effect on plant  
556 community response was found in this study. The strongest examples of synergism were  
557 observed in the rates of photosynthetic electron transport in the Bryophyte and *Usnea*  
558 communities, where although some increases were observed in response to water and nutrient  
559 additions when applied singularly, the highest rates occurred when both water and nutrients  
560 were added (Fig. 2A). Also, a trend toward synergism was observed for total chlorophyll in  
561 the Crustose and *Usnea* communities, where total chlorophyll concentrations were highest in  
562 the combined water and nutrient treatments (Fig. 2B). This result was surprising since it  
563 shows that sufficient water is available for most communities - except perhaps the driest,  
564 *Usnea* - to take up additional nutrients when they are available, rather than water plus  
565 nutrients being required to elicit this response.

## 566 **Conclusions**

567 This study represents one of the only manipulative field experiments to be conducted in  
568 continental Antarctica, and illustrates both that such studies are possible and can provide  
569 valuable information regarding the way in which Antarctic terrestrial communities are likely  
570 to respond to climate change. Primary productivity surrogates showed an overall increase in  
571 response to water and nutrient additions, but appeared to respond more strongly to nutrients  
572 than to water. Certain communities are likely to thrive under a wetter future, provided nutrient  
573 availability increases with increasing water availability. Increased productivity was most  
574 pronounced in the Crustose and Bryophyte communities, suggesting these community types  
575 may be most able to adapt and prosper under the ameliorating conditions associated with a  
576 warmer, wetter future climate. However, if nutrient availability does not increase along with  
577 wetter conditions, bryophyte communities may be nutrient-limited and fail to thrive.

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740 **Tables**

741 **Table 1:** Summary of 2-way ANOVA results for total chlorophyll concentration (Total Chl),  
 742 electron transport rate (ETR), turf water content (TWC), % Nitrogen (%N), % Phosphorous  
 743 (%P) and nitrogen and carbon stable isotopic signatures ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ).

<b>Variable</b>	<b>Transformation</b>	<b>Test</b>	<b>DF (model, error)</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Total Chl	Log10	Whole Model	15, 96	5.3245	<0.0001
		Treatment	3	10.4628	<0.0001
		Community	3	13.6611	<0.0001
		Treatment x Community	9	0.8329	0.5876
ETR	None	Whole Model	15, 80	8.5041	<0.0001
		Treatment	3	16.6085	<0.0001
		Community	3	13.7313	<0.0001
		Treatment x Community	9	4.0602	0.0003
TWC	Log 10	Whole Model	15, 96	1.7162	0.0602
		Treatment	3	0.9719	0.4093
		Community	3	6.0204	0.0008
		Treatment x Community	9	0.5295	0.8498
% N	Log10	Whole Model	15, 81	17.5206	<0.0001
		Treatment	3	12.9166	<0.0001
		Community	3	68.3384	<0.0001
		Treatment x Community	9	2.1529	0.034
% P	Square Root	Whole Model	15, 82	14.553	<0.0001
		Treatment	3	1.1904	0.3186
		Community	3	68.1251	<0.0001
		Treatment x Community	9	1.102	0.3707
$\delta^{15}\text{N}$	Log 10	Whole Model	15, 82	2.8606	0.0012
		Treatment	3	0.6365	0.5936
		Community	3	11.9305	<0.0001
		Treatment x Community	9	0.5974	0.7957
$\delta^{13}\text{C}$	None	Whole Model	15, 82	19.8089	<0.0001
		Treatment	3	0.9378	0.4263
		Community	3	93.0691	<0.0001
		Treatment x Community	9	0.7446	0.6671

744 **Figure Legends**

745 **Figure 1:** Position within the site and distinguishing characteristics of the four communities  
746 types used in the field water and nutrient enrichment experiment. The meltlake is to the left  
747 and the abandoned rookery ridge to the right of the main photo. Percent cover was estimated  
748 using a 25x25 cm quadrat. *Grimmia antarctici* is the dominant bryophyte species across site.

749 **Figure 2:** Influence of the four water and nutrient treatments on (A) photosynthetic electron  
750 transport rate (ETR;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and (B) total chlorophyll concentration ( $\text{nmol g}^{-1} \text{dw}$ ) for  
751 plant material from the four experimentally manipulated communities (Bryophyte, Moribund,  
752 Crustose and *Usnea*) after two seasons treatment with water, nutrients, water plus nutrients or  
753 no treatment. Bars represent mean  $\pm$  sem, n = 6 (A) n = 7 (B).

754 **Figure 3:** Influence of the four water and nutrient treatments on (A) turf water content (TWC;  
755  $\text{g H}_2\text{O g}^{-1} \text{dw}$ ), (B) percent N (C) percent P and (D)  $\delta^{13}\text{C}$  (‰) signature, for plant material  
756 from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and  
757 *Usnea*). Samples were collected after 15 months treatment with water, nutrients, water plus  
758 nutrients or no treatment. Bars represent mean  $\pm$  sem, n = 5-7. Note y-axes scales are  
759 different.

# Figures

Figure 1:

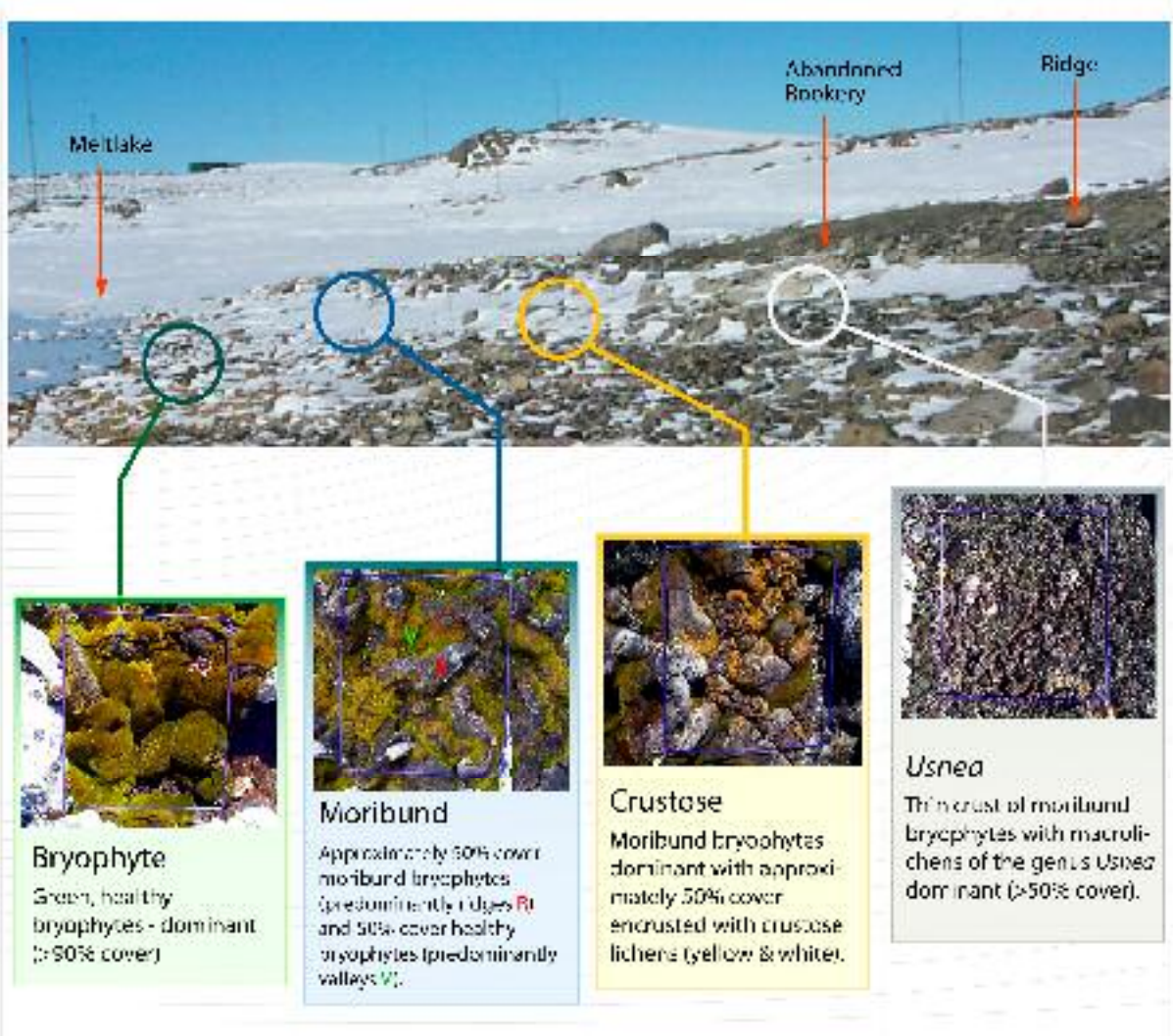


Figure 2:

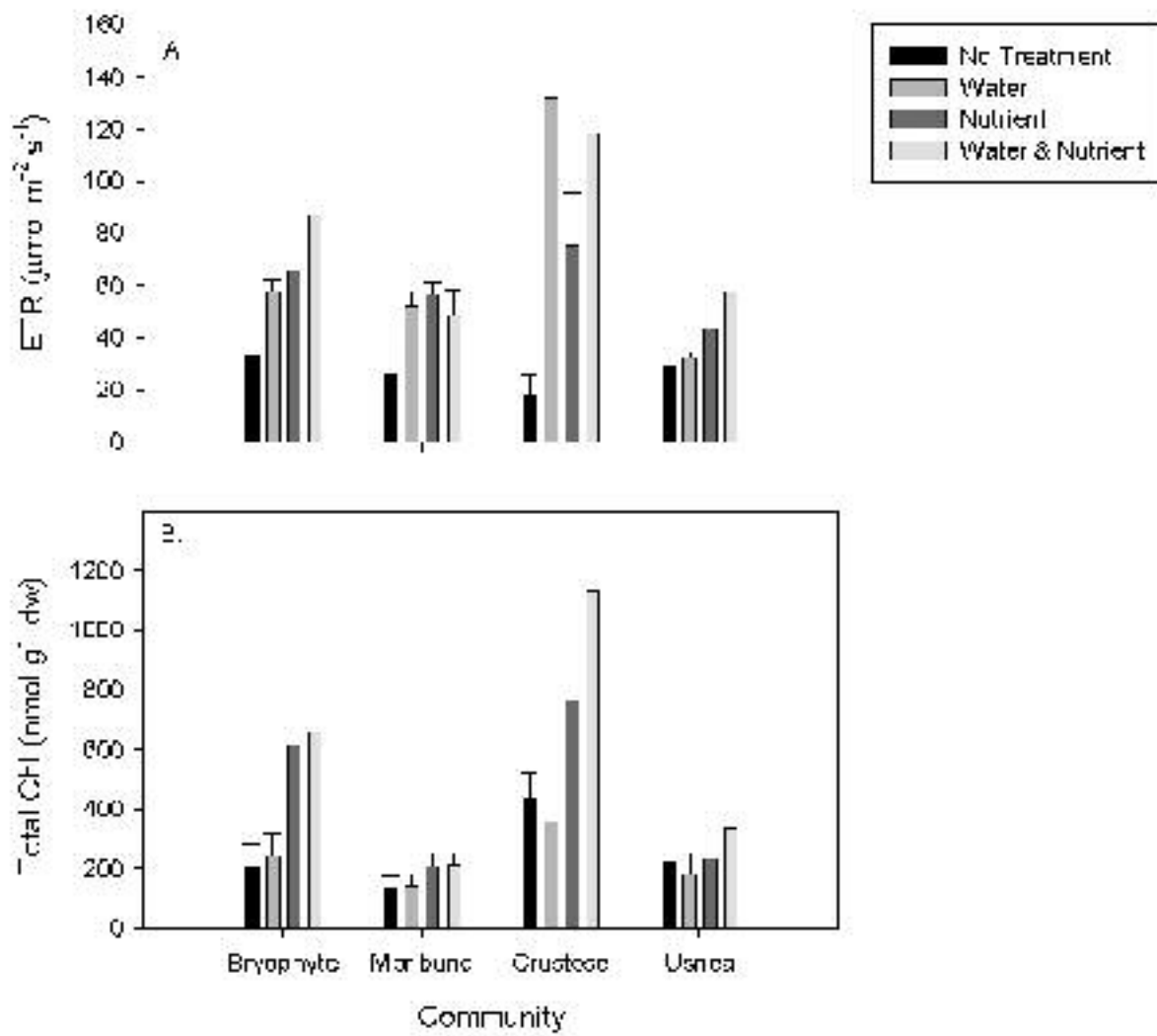


Figure 3:

