

1 **Invited Review: Climate change impacts in polar-regions: lessons**
2 **from Antarctic moss bank archives**

3 **Running head:** Lessons from Antarctic moss banks archives

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11 **Keywords:** Stable isotopes; climate change; Antarctic moss; radiocarbon dating; peat
12 accumulation; assimilation

13 **Abstract:**

14 Mosses are the dominant plants in polar and boreal regions, areas which are experiencing
15 rapid impacts of regional warming. Long-term monitoring programmes provide some records
16 of the rate of recent climate change, but moss peat banks contain an unrivalled temporal
17 record of past climate change in terrestrial plant Antarctic systems. We summarise the current
18 understanding of climatic proxies and determinants of moss growth for contrasting
19 continental and maritime Antarctic regions, as informed by ¹³C and ¹⁸O signals in organic
20 material. Rates of moss accumulation are more than three times higher in the maritime
21 Antarctic than continental Antarctica with growing season length being a critical determinant

22 of growth rate, and high carbon isotope discrimination values reflecting optimal hydration
23 conditions. Correlation plots of ^{13}C and ^{18}O values show that species (*Chorisodontium*
24 *aciphyllum* / *Polytrichum strictum*) and growth form (hummock / bank) are the major
25 determinants of measured isotope ratios. The interplays between moss growth form,
26 photosynthetic physiology, water status and isotope composition are compared with
27 developments of secondary proxies, such as chlorophyll fluorescence. These approaches
28 provide a framework to consider the potential impact of climate change on terrestrial
29 Antarctic habitats as well as having implications for future studies of temperate, boreal and
30 Arctic peatlands. There are many urgent ecological and environmental problems in the Arctic
31 related to mosses in a changing climate, but the geographical ranges of species and life-forms
32 are difficult to track individually. Our goal was to translate what we have learned from the
33 more simple systems in Antarctica, for application to Arctic habitats.

34

35 **1. Introduction**

36 Global climate is changing, with heterogeneous effects on the biological world including
37 direct impacts on plant phenology. The resilience and future dynamics of ecosystems will
38 depend on their responsiveness to gradual environmental change, as well as susceptibility to
39 more frequent climatic extremes (e.g. Orsenigo *et al.*, 2014, Xu *et al.*, 2013). High latitude
40 regions are experiencing particularly rapid climatic changes, and bryophytes, specifically
41 mosses, are the dominant plants in both the Arctic and the Antarctic. Wetlands cover 70% of
42 the Arctic, largely made up of *Sphagnum* dominated peatlands that are shaped by freeze-thaw
43 processes and may be minerotrophic fens or ombrotrophic bogs (Minayeva & Sirin, 2010).
44 In the Antarctic, over one hundred species of moss have been identified (Ochyra *et al.*, 2008),
45 with two native vascular plant species. Most Antarctic mosses form occasional low growing

46 carpets, mats, turfs and hummocks, whilst some ombrotrophic peat banks up to three metres
47 deep have accumulated in more maritime areas.

48 Global peatlands contain approximately 600 Pg of stored carbon (Yu *et al.*, 2010) but they
49 are under threat across high latitude regions (Gallego-Sala & Prentice, 2013), with
50 potentially significant impacts on the global carbon cycle (McGuire *et al.*, 2009). Therefore,
51 incorporating moss dynamics into vegetation models is essential (Turetsky *et al.*, 2012) and
52 understanding the bryophytes within the simple ecosystem context of Antarctica, in
53 combination with contemporary bryophyte physiology, can provide important lessons
54 applicable to more complex Arctic habitats.

55 This review firstly summarizes the climate, vegetation and growth dynamics of Antarctic
56 moss-peat accumulations before considering the current understanding of climatic proxies,
57 particularly focussing on the use of stable isotope analysis of preserved organic material, and
58 contrasting responses between continental and maritime regions. The interplay between moss
59 photosynthetic physiology, water status and growth-form are compared with recent
60 developments of secondary proxies (such as ^{13}C and ^{18}O in organic material). These
61 approaches provide a framework to consider the potential impact of climate change on the
62 growth and distribution of Antarctic mosses, and the future of temperate, boreal and Arctic
63 peatlands. Finally, we explore the need for additional experimental validation of these
64 proxies, and consider developments which could facilitate future monitoring of moss banks
65 under a changing climate.

66 ***Poles apart: contrasting diversity and climatic impacts upon high latitude vegetation***

67 Both polar-regions experience low mean annual temperatures, seasonal extremes in day
68 length and often have low free water availability. At high northern latitudes recent
69 temperatures are unprecedented over at least the last 600 years (Tingley & Huybers, 2013),

70 and the maritime Antarctic Peninsula (AP), the most vegetated area of Antarctica, has been
71 one of the most rapidly warming regions on Earth (Turner *et al.*, 2009). As winter
72 temperatures increase more rapidly than summer temperatures, polar seasonality has
73 decreased (Franzke, 2012, Xu *et al.*, 2013), and permafrost distribution has altered
74 (Bockheim *et al.*, 2013, Guglielmin *et al.*, 2014, Quinton *et al.*, 2011, Turetsky *et al.*, 2007)
75 which is expected to have significant effects on the global carbon budget (Koven *et al.*, 2011,
76 Schuur *et al.*, 2009). Earlier annual melting of both northern (Surdu *et al.*, 2014) and southern
77 (Quayle *et al.*, 2002) polar lakes indicates a potential lengthening of the biological growing
78 season. Despite the similar physical responses of the poles to warming, the contrasting
79 relative geographical isolation of Arctic and Antarctic terrestrial ecosystems have generated
80 substantial differences in past, present and likely future floral diversity.

81 Antarctic vegetation is limited to Southern Ocean islands, areas of the AP, rare ice-free
82 locations around the continent's perimeter and occasional interior nunataks. Seasonally snow-
83 and ice-free ground comprises only 0.34% of the total continental area (Convey *et al.*, 2009).
84 The isolation of Antarctica, separated from land masses by the Southern Ocean, Antarctic
85 Circumpolar Current and Southern Westerly Wind belt (Barnes *et al.*, 2006) is in contrast to
86 the Arctic, where the continuity of Eurasia and North America has facilitated the
87 development of more complex ecosystems. Along with substantial vascular plant diversity
88 (1800 species), 600 moss species are found in the Arctic, which represents over 4% of global
89 diversity (Callaghan *et al.*, 2005). Bryophytes are poikilohydric plants with little capacity to
90 buffer changes in water availability, so periods of metabolic activity are tightly coupled to
91 microclimatic conditions (Longton, 1988, Royles *et al.*, 2013b, Schlensoeg *et al.*, 2013,
92 Wasley *et al.*, 2006). Consequently, preserved bryophyte tissue has the potential to provide
93 an archive of local conditions at the time of active photosynthesis (Clarke *et al.*, 2012, Royles
94 *et al.*, 2012).

95 *Bryophytes as polar palaeoclimate recorders*

96 Given the scarcity of plant monitoring programmes in Antarctica (Wall *et al.*, 2011),
97 permafrost-preserved moss peat deposits contain an unrivalled temporal biological record.
98 These ombrotrophic peat banks, comprised of *Chorisodontium aciphyllum* (Brotherus) and/or
99 *Polytrichum strictum* (Bridwell), can date from over 5000 years ago (Björck *et al.*, 1991b,
100 Fenton, 1980) and multi-proxy analyses provides information about the past environment
101 along with insights for the likely responses to a changing climate. As moss growth is entirely
102 dependent on enzymatic processes, tempered by liquid water availability, peat cores provide
103 unequivocal evidence of periods during which environmental conditions were suitable for
104 photosynthesis. Globally, mining the information stored in stratigraphic peat deposits has
105 allowed significant advances in the understanding of past environments via reconstruction of
106 vegetation history from pollen and higher plant remnants in combination with absolute
107 accumulation rates derived from age-depth profiles (e.g. Chambers *et al.*, 2011, Charman *et*
108 *al.*, 2013, Piotrowska *et al.*, 2011).

109 **2. Distribution, past change and possible future dynamics of maritime**

110 **Antarctic peat banks**

111 The majority of high latitude Southern Hemisphere peatlands are in Patagonia, however they
112 comprise only 1% of the global peatland area (Yu *et al.*, 2010). Patagonian peatlands
113 experience a climate with low precipitation and mild temperatures, and this minimal
114 seasonality facilitates a long, potentially continuous, growing season (Loisel & Yu, 2013,
115 Smith & Clymo, 1984). Peat addition rates are high, as conditions favour long periods of
116 assimilatory carbon gain, whilst decomposition is limited by low summer temperatures
117 (Loisel & Yu, 2013). Significant peat accumulations are also present on several sub-

118 Antarctic islands (Van der Putten *et al.*, 2012), with this region again being characterised by
119 limited seasonality in many environmental variables (Convey, 2013).

120

121 Further south, Antarctic peat banks are characterised by the absence of vascular plant
122 material, the dominance of *C. aciphyllum*, or *P. strictum* in drier areas, and slow
123 accumulation rates of approximately 1 mm yr⁻¹ (Fenton & Smith, 1982, Smith & Corner,
124 1973). The most significant banks are located within the Antarctic Peninsula and Scotia Arc,
125 between Signy Island (60°S, South Orkney Islands) (Fenton, 1980, Smith, 1972) and
126 Elephant Island (61°S, South Shetland Islands) (Björck *et al.*, 1991b) in the north, and
127 Alexander Island (Convey *et al.*, 2011, Royles *et al.*, 2013a) (69°S) in the south (Figure 1). In
128 comparison with the peat deposits of the sub-Antarctic islands (Van der Putten *et al.*, 2012)
129 and Patagonia (Loisel & Yu, 2013), which have higher species diversity, there are both
130 advantages and disadvantages to the use of cores from Antarctic moss peat banks as
131 palaeoclimate archives. Mono- or bi-specific cores in which species can be readily identified
132 facilitate chemical analysis without the need for subsequent separation of species effects from
133 climate effects. However, the low diversity precludes direct interpretation of change to
134 species composition as an indicator of environmental conditions. With the presence of
135 permafrost below c. 30 cm depth (Fenton, 1980, Guglielmin *et al.*, 2012) and little microbial
136 activity (Block, 1984, Convey, 2001) within the active layer, peat compression and
137 decomposition are minimal. Consequently, organic matter is extraordinarily well preserved in
138 the Antarctic banks, to the extent that 1500 year old moss shoots have recently been shown to
139 regenerate spontaneously in the laboratory (Roads *et al.*, 2014).

140

141 The appropriate interpretation of palaeoclimate archives in the context of broader spatial and
142 temporal changes requires accurate methods for dating material. The purity and cryo-

143 protection of moss shoots, the absence of roots and minimal translocation of substances
144 makes moss peat ideal material for accurate radiocarbon dating (Björck *et al.*, 1991a). Dating
145 of basal peat provides a minimum date at which conditions became suitable for net
146 assimilation following the Last Glacial Maximum (LGM). The Antarctic moss banks vary in
147 their age, accumulation rate and continuity, with the oldest known banks on Elephant Island
148 ($61^{\circ}08'S$ $054^{\circ}42'W$) dating back over 5000 years (Björck *et al.*, 1991b). The new date for the
149 base of the peat at Norsel Point, Anvers Island ($64^{\circ}45'S$ $064^{\circ}05'W$), 620 km SW of Elephant
150 Island suggests accumulation for at least 1500 years, whilst at the southernmost site, a further
151 600 km SSW on Alexander Island ($69^{\circ}22'S$ $71^{\circ}51'W$) the basal date shows that net
152 accumulation began within the last two centuries (Figure 1b).

153 The restricted distribution of moss peat banks demonstrates that, whilst permanently ice free
154 ground is essential for their establishment, it is by no means sufficient. Fenton and Smith
155 (1982) identified eight factors (i-viii, below) that determine the extent of an Antarctic moss
156 bank. Thirty years on, we re-assess each of these factors in terms of establishment,
157 maintenance and accumulation.

158 ***i) Length of time the ground is snow-free in summer***

159 Moss requires snow and ice-free ground on which to establish, and, although limited
160 photosynthesis can occur through some snow cover as long as the tissue has thawed
161 (Longton, 1988), the majority of net assimilation will occur following the spring snow melt.
162 The length of time that the ground is snow-free in summer has generally increased. On Signy
163 Island, ice cover reduced by 45% between 1950 and 1990 (Smith, 1990), and freshwater
164 lakes are annually ice-free for an additional two months (Quayle *et al.*, 2002), both of which
165 are proxies for an increase in the length of the biologically active season (Block & Convey,
166 2001). This has been reflected in the growth rates of *C. aciphyllum* moss banks on Signy

167 Island which increased from a maximum of 2.4 mm y⁻¹ in 1976 (Fenton, 1980) to 3.9 mm y⁻¹
168 in 2009 despite windier and wetter summers reducing the instantaneous photosynthetic
169 assimilation rate (Royles *et al.*, 2012).

170 ***ii) Length of time the ground has been free from permanent snow and ice cover***

171 The AP and surrounding islands were ice covered during the LGM. Currently approximately
172 3.6% (4300 km²) of the land area of the AP, South Orkney and South Shetland Islands is ice-
173 free (Peat *et al.*, 2007), an essential requirement for the establishment of moss. The retreat of
174 87% of AP glacier termini and reduced permanent snow cover (Cook *et al.*, 2005, Strauss *et*
175 *al.*, 2009) provides land on which new moss banks could establish, and may re-expose moss
176 tissue that can spontaneously regenerate new growth (LaFarge *et al.*, 2013; Roads *et al.*,
177 2014). Rapid glacier retreat on Ellesmere Island, Canada revealed viable bryophyte
178 assemblages that had been buried under ice for up to 400 years (La Farge *et al.*, 2013).
179 Laboratory experiments show that Antarctic *C. aciphyllum* has the capacity for regrowth
180 from shoots at least 1500 years old (Roads *et al.*, 2014). Although photosynthesis can occur
181 through a limited snow covering, changes in snow cover patterns over time could explain
182 periods of very slow / negligible peat accumulation that are evident in some age-depth
183 models (e.g. Björck *et al.*, 1991b, Royles *et al.*, 2012), but the capacity for re-establishment
184 of growth following subsequent alterations to snow distribution is also becoming clear.

185 ***iii) Stability of the substratum***

186 Moss banks require stable rock or soil in order to establish and accumulate (Fenton & Smith,
187 1982) so volcanic soils, areas undergoing substantial frost heave and beaches are unsuitable.
188 Changes in the extent and depth of permafrost will impact the stability of the substratum
189 more rapidly than substantial geological changes. On Signy Island, the active layer thickness
190 is projected to increase at 10 mm yr⁻¹ (Cannone *et al.*, 2006). In 1976 the depth of seasonal *C.*

191 *aciphyllum* bank thaw was 210 ± 10 mm (Fenton, 1980), by 2009 the thaw in the same banks
192 was 300 ± 10 mm (Royles *et al.*, 2012). This 40% increase in seasonally unfrozen biomass was
193 coincident with an increase in mean annual temperature (MAT) of 0.9°C (Quayle *et al.*,
194 2002); however, there can be substantial inter-annual variation in permafrost depth
195 (Guglielmin *et al.*, 2014). Further south, in Victoria Land, continental Antarctica the active
196 layer depth has increased at approx. 0.3 cm yr^{-1} since 2000, which has altered soil stability
197 and decreased water availability to mosses (Guglielmin *et al.*, 2014).

198 ***iv) Biotic disturbance***

199 Growing slowly without strong attachment to the substratum, moss will not successfully
200 establish on frequently disturbed ground. Established moss banks are vulnerable to erosive
201 damage by both abiotic and biotic agents and are increasingly at risk as the depth of the
202 active layer increases (see above). Fur seals (*Arctocephalus gazella*) cause physical damage
203 to terrestrial ecosystems (Smith, 1988a), which is evident on Signy Island where 73% land is
204 covered with bryophytes in areas without seal pressure compared with 1.7% of land in areas
205 with high seal pressure (Favero-Longo *et al.*, 2011). Thus, whilst potentially increasing
206 nutrient availability, a recent eight-fold increase in the fur seal population (1600 in 1978,
207 12600 in 2008) (Waluda *et al.*, 2010) has negative consequences for the establishment and
208 maintenance of moss banks.

209 ***v) Harshness of the environment – i.e. exposure***

210 Antarctica is windy: on the South Shetland Islands the mean wind speed is 26 km hr^{-1} , with
211 gusts frequently over 100 km hr^{-1} (Bañón *et al.*, 2013). Furthermore, summer and autumn
212 wind speeds significantly increased (by 7-27% in summer) between 1980 and 2002 in the
213 latitude band from 50 to 65°S (Korhonen *et al.*, 2010). With increased wind speed the rate of
214 erosion is likely to increase (especially with the increased depth of the active layer), and the

215 rate of evaporation will increase from the surface of soils and mosses. Although the mass of a
216 bank largely buffers the overall water content (Gimingham & Smith, 1971), if the surface
217 water film evaporates, the growing apices may become increasingly water limited and
218 desiccated.

219 **vi) Nutrient status**

220 Animal colonies provide important nutrient inputs to terrestrial ecosystems, both directly, and
221 indirectly from wet and dry atmospheric deposition (Bokhorst *et al.*, 2007). There have been
222 substantial changes in animal populations and distributions over the past 30 years in the AP
223 region. Populations of chinstrap (*Pygoscelis antarctica*) and Adélie (*Pygoscelis adeliae*)
224 penguins have decreased, whilst gentoo (*Pygoscelis papua*) penguin and fur seal populations
225 have increased (Lynch *et al.*, 2012, Waluda *et al.*, 2010) which may alter local nutrient
226 distribution. In addition to changes in nutrient availability, there is potentially increased
227 competition for nutrient uptake as the vascular plant *Deschampsia antarctica* is able to take
228 up amino acids directly through its roots and thus acquire nitrogen over 160 times more
229 quickly than Antarctic mosses (Hill *et al.*, 2011) and this efficient uptake and usage may be a
230 mechanism by which the Antarctic vascular plants out-compete bryophytes in the long term.

231 **vii) Water supply**

232 The form and timing of precipitation are critical to the establishment, growth and
233 development of plants. Indeed, water supply is the most important physical driver of
234 Antarctic terrestrial communities and limits floral distribution across the continent (Convey *et*
235 *al.*, 2014). Across the maritime Antarctic precipitation is frequent, with an increasing
236 proportion falling as rain rather than snow; however, water availability can vary very locally
237 which has a significant impact on the metabolic activity of plants (See sections 4&5)
238 (Schlensog *et al.*, 2013, Wasley *et al.*, 2012). The capacity for capillarity may limit the depth

239 to which poikilohydric moss tissue can accumulate as exposed growing tips lose water
240 through evaporation (Melick & Seppelt, 1997).

241 **viii) Slope**

242 With the depth of the active layer deepening, the wind strengthening and increased summer
243 rain, moss banks are more vulnerable to erosion, slumping and collapse. After loss of the top
244 section, the newly-exposed surface moss may resume growth, or be invaded by epilithic
245 lichens, other mosses, or provide an environment for vascular plant growth (Fabiszewski &
246 Wojtun, 1997).

247 In conclusion, the preceding analyses suggest that, whilst some edaphic factors may limit
248 colonisation and moss bank formation/degradation, other factors associated with climate
249 change, such as an extended growing season and altered precipitation patterns may help to
250 enhance carbon accumulation overall. We now consider the implications for moss bank
251 growth, and specifically compare the drivers for the contrasting extent of peat accumulation
252 across Antarctica.

253

254 **3. Moss accumulation rates across Antarctica**

255 Fewer than 30 species of the known moss flora of Antarctica have been identified south of
256 67°S, and none are currently thought to be endemic to the very cold and dry continental
257 region (Ochyra *et al.*, 2008, Peat *et al.*, 2007). Whilst across the AP diversity decreases at
258 higher latitudes (Peat *et al.*, 2007), the continental distribution of plants suggests that it is
259 local microclimate conditions, particularly water availability, that are critical in determining
260 floral diversity (Cannone *et al.*, 2013, Colesie *et al.*, 2014, Convey *et al.*, 2014, Green *et al.*,
261 2011). Vegetation surveys across Antarctica have been very limited spatially and temporally,

262 with basic species presence and proportion cover records mainly focussed around research
263 stations (Chown & Convey, 2007). It is rare for the depth of moss growth to be recorded; *in*
264 *situ* experimental systems, to measure rates of moss growth, are difficult to establish and
265 repeat visits to assess changes are rare. Consequently, there is limited baseline information
266 available on Antarctic bryophytes from which any past or future effects of climate change can
267 be assessed.

268

269 The best studied terrestrial vegetation in continental Antarctica is from the Windmill Islands
270 region in East Antarctica, where three moss species (*Schistidium antarctici* (Cardot), *Bryum*
271 *pseudotriquetrum* (Hedwig) and *Ceratodon purpureus* (Hedwig)) are found (Melick &
272 Seppelt, 1997, Robinson *et al.*, 2000, Wasley *et al.*, 2012). Areas of moribund moss suggest
273 that vegetation has changed, but it is difficult to determine the timing of moss establishment
274 due to fungal contamination compromising radiocarbon dating. Direct measurement of moss
275 growth using tags is problematic due to the low growth rates (<7 mm in four growing
276 seasons) and loss of tags (Melick & Seppelt, 1997).

277

278 The uneven species' distribution across Antarctica complicates the comparison between moss
279 growth in the eastern and western regions, but the responses do provide contrasting markers
280 for different life forms and climatic extremes. In the absence of detailed laboratory
281 comparisons of physiology and growth under controlled environment conditions, we feel this
282 broad comparison is informative. Whilst the moss peat accumulations in the maritime
283 Antarctic region reach a maximum depth of 3 m on Elephant Island (Björck *et al.*, 1991b),
284 the continental Antarctic moss associations rarely reach 10 cm (Melick & Seppelt, 1997).
285 Combining published age-depth profiles from moss accumulations from the Windmill
286 Islands (Clarke *et al.*, 2012), with those from Lazarev Bay (Convey *et al.*, 2011, Royles *et al.*,

287 2013a) and Signy Island (Royles *et al.*, 2012) since 1960 it is apparent that the rate of moss
288 organic matter accumulation in the maritime Antarctic is at least three times higher than that
289 in continental Antarctica (Figure 3).

290 Within the continental Antarctic mosses, the accumulation of *C. purpureus* in the
291 Windmill Islands, which prefers drier habitats (Robinson *et al.*, 2000), is slower than that of
292 the more mesophytic *B. pseudotriquetrum* and *Bryoerythrophyllum recurvirostre* (Hedwig)
293 from the Vestfold Hills (Clarke *et al.*, 2012). Compression and decomposition are not taken
294 into account, but as the measurements are made on individual shoots up to only 50 mm long,
295 the effects of both processes are minimal. In the maritime Antarctic region, the similarity in
296 accumulation rate between the Lazarev Bay and Signy Island banks since 1960 is interesting,
297 as they lie at opposite extremes of the distribution range, approximately 1500 km apart, and
298 are comprised of *P. strictum* and *C. aciphyllum* respectively. At both locations the top 100
299 mm of peat, within which zone compression will be minimal, has accumulated since 1988, at
300 approximately 4 mm yr⁻¹. Using bulk density measurements, the peat accumulation rate at
301 Signy Island can be compared with that previously published at Lazarev Bay (Figure 4;
302 (Royles *et al.*, 2013a)). Whilst accumulation reached a peak at Lazarev Bay in the 1970s
303 (briefly over 0.1 g DM cm⁻² yr⁻¹, when smoothed over three successive time-points), the rate
304 at Signy Island reached a peak in the 1990s, at 0.06 g DM cm⁻² yr⁻¹. Both start to increase
305 from around 1950 and the most recent measurements are similar at around 0.04 g DM cm⁻²
306 yr⁻¹. Similarly in continental Antarctica, where moss growth rate was inversely proportional
307 to summer wind-speed, and proportional to the number of days above 0°C and to summer
308 temperature, the Windmill Island mosses had maximum growth rates in the 1950s-1980s that
309 subsequently fell in the 90s and 00s. However, at the Vesfold Hills the most recent moss
310 growth rates have been highest (Clarke *et al.*, 2012). The length of the growing season is a
311 critical determinant of moss growth rate in both continental (Clarke *et al.*, 2012) and AP

312 locations (Royles *et al.*, 2012). The length of past growing seasons cannot be determined
313 directly from moss-cores, but estimates have been made by combining accumulation rates
314 derived from radiocarbon dating with stable isotope proxies for assimilation rate (Royles *et*
315 *al.*, 2012).

316 **4. Isotope proxies preserved in Antarctic moss over space and time**

317 Stable isotopes provide natural markers for the environmental control of metabolic reactions
318 (Dawson *et al.*, 2002, Farquhar *et al.*, 1989). Analyses of ^{13}C or ^{18}O , relative to the more
319 common isotopomers (^{12}C or ^{16}O), when preserved in tree rings and peat cores, are widely
320 used as environmental tracers that provide information about past growth conditions, with
321 work published from Canada (e.g. Daley *et al.*, 2011, Kaislahti Tillman *et al.*, 2010) and
322 northern Europe (e.g. Daley *et al.*, 2010, Loader *et al.*, 2008, Ménot-Combes *et al.*, 2002,
323 Ménot & Burns, 2001). More recently the ^{13}C , ^{18}O and ^2H composition of cellulose, organic
324 matter and source water have been used to quantify responses of Antarctic moss to climate
325 change (Clarke *et al.*, 2012, Royles *et al.*, 2013a, Royles *et al.*, 2012, Royles *et al.*, 2013c).

326 Mass-dependent “kinetic” fractionation of isotopes occurs either between the reactants and
327 products of a unidirectional reaction or during diffusion, whilst “equilibrium” fractionation is
328 the partial separation of isotopes between substances or phases in chemical equilibrium.
329 Heavy isotopic species (e.g. $^{13}\text{CO}_2$ or H_2^{18}O) tend to react more slowly and usually become
330 enriched in a denser equilibrium phase, or depleted during a kinetic transformation, and thus
331 provide important biomarkers (Farquhar *et al.*, 1989). The ratio (R) of heavy to light isotopic
332 species (e.g. $R_{\text{SAMPLE}} = ^{13}\text{CO}_2/^{12}\text{CO}_2$) is usually measured via high-precision mass
333 spectrometry, compared to a known standard (R_{STANDARD}) and presented as a differential (δ)
334 notation, such as a $\delta^{13}\text{C}$ value:

$$335 \quad \delta^{13}\text{C} = (R_{\text{SAMPLE}}/R_{\text{STANDARD}}) - 1$$

336 Source independent photosynthetic carbon isotope discrimination ($\Delta^{13}\text{C}$) can then be derived,
337 if $\delta^{13}\text{C}$ values are known for both the plant ($\delta^{13}\text{C}_p$) material and the source CO_2 , usually
338 atmospheric CO_2 ($\delta^{13}\text{C}_a$):

$$339 \quad \Delta^{13}\text{C} = \delta^{13}\text{C}_a - \delta^{13}\text{C}_p / 1 + \delta^{13}\text{C}_p \text{ (Farquhar } et al., 1989).$$

340 $\Delta^{13}\text{C}$ is dominated by the biochemical fractionation of the carboxylase enzyme RuBisCO,
341 having a value of around 29‰ in C_3 plants (O'Leary, 1988). This maximal fractionation is
342 proportionally inhibited by resistance to CO_2 diffusion, leaving assimilates (and subsequently
343 plant tissue) ^{13}C -depleted compared to atmospheric, source CO_2 inputs. In astomatous
344 bryophytes, the external water layer is a critical determinant of diffusion resistance and,
345 consequently, the extent of discrimination against $^{13}\text{CO}_2$. Real-time measurements on
346 liverworts, *Sphagnum* moss and *Syntrichia ruralis* show that a reduction in the external water
347 layer is associated with an increase in instantaneous discrimination against $^{13}\text{CO}_2$ and in
348 assimilation rate (Meyer *et al.*, 2008, Rice & Giles, 1996, Royles *et al.*, 2013b, Williams &
349 Flanagan, 1996). As a proportion of the assimilated carbon is used to synthesise the structural
350 carbohydrate cellulose, a major degradation-resistant component of bryophyte organic matter,
351 the carbon isotope ratio of moss cellulose ($\delta^{13}\text{C}_C$) is a good proxy of the assimilation
352 conditions during photosynthesis (Royles *et al.*, 2012). Antarctic moss tissue $\delta^{13}\text{C}$ values are
353 dependent on wind speed, temperature (both of which influence water availability) and ozone
354 depth (which is linked to the phase of the Southern Annular Mode, and, consequently, wind-
355 speed) (Clarke *et al.*, 2012, Robinson & Erickson III, in press).

356 Measurements of the ^{13}C composition of Antarctic moss have been carried out on different
357 species (including *P. strictum*, *C. aciphyllum* and *C. purpureus*), with different growth habits
358 (large banks, hummocks and small cushions), with concurrent measurements back to the
359 1960s (Clarke *et al.*, 2012, Royles *et al.*, 2013a, Royles *et al.*, 2012). Whilst $\delta^{13}\text{C}$ was

360 measured in whole organic matter for *C. purpureus*, most measurements on *C. aciphyllum*
361 and *P. strictum* were made on cellulose; however, comparative measurements of organic
362 matter and cellulose had a highly significant linear relationship (Royles, 2012) so $\delta^{13}\text{C}_{\text{OM}}$
363 measurements could be derived. Over the 60 y period under consideration in these
364 environments in which the rate of degradation is low, the compound specific diagenetic
365 effects that are an important factor to consider over long time periods should not be
366 substantial. There is a significant depletion in the composition of all the moss tissue over
367 time due to the assimilation of atmospheric CO_2 which is globally becoming more depleted
368 following the combustion of fossil fuels (Figure 5a) (Friedli *et al.*, 1986).

369 Source-independent $\Delta^{13}\text{C}$ was calculated for each measurement (Farquhar *et al.*, 1989),
370 dependent upon the isotopic composition of atmospheric CO_2 (Rubino *et al.*, 2013) at the
371 time of synthesis (as derived from ^{14}C measurements and estimated from age-depth model;
372 (Figure 5b)). Any contribution to assimilated carbon from sources of respiratory CO_2 , such as
373 those associated with microbes or moss decay, were not included in the calculation of $\Delta^{13}\text{C}$.
374 Overall rates of respiration and microbial metabolism are low (Royles *et al.*, 2013a) and the
375 exposed banks are generally well-coupled to the atmosphere in the prevailing windy
376 conditions. Were any respiratory CO_2 , with a source isotope composition close to that of bulk
377 material, to be refixed, it would tend to slightly increase the $\Delta^{13}\text{C}$ values to a similar extent at
378 all water contents. This response is not consistent with the declining $\Delta^{13}\text{C}$ seen in Signy
379 Island moss banks (Royles *et al.*, 2012), associated with warmer and wetter growth (and
380 presumably higher respiration rates) over the past decade.

381 Despite the species variation and geographic separation of up to 5000 km between sites, the
382 measured $\Delta^{13}\text{C}$ values are very similar, covering a 4‰ range from 17 to 21‰. The Lazarev
383 Bay moss had the highest source independent discrimination with the exception of 1970
384 when one *C. purpureus* value was higher. The lowest discrimination values of 17‰ were

385 measured on Signy Island, with the three *C. purpureus* and three *C. aciphyllum* cores largely
386 overlapping in values between 17‰ and 20‰. When the Signy Island and Lazarev Bay
387 $\Delta^{13}\text{C}_\text{C}$ values are considered back to 1850, the Lazarev Bay values show higher
388 discrimination, which could be due to the species effect i.e. the Signy core is comprised of *C.*
389 *aciphyllum*, whilst the Lazarev core is *P. strictum*, two species which have different
390 anatomies and external water layers, along with potentially different metabolic responses to
391 environmental conditions. In all the cores, the source independent discrimination was higher
392 in 2000 than at the start of the record, with one of the Signy Island cores showing a 3‰
393 increase, with a 2‰ range at Lazarev and 1.5-2‰ elsewhere on Signy. On Signy Island the
394 majority of the increase in $\Delta^{13}\text{C}$ occurred prior to 1960, compared with the substantial
395 increase being measured from 1960 onwards at Lazarev Bay.

396 Higher discrimination values generally suggest more optimal conditions of hydration, when
397 photosynthetic carbon is fixed during periods of minimal diffusion limitation (i.e. neither too
398 wet nor too dry). At both Signy Island and Lazarev Bay there has been a tendency for a
399 reduction in the measured values most recently, with highest discrimination in the mid 1990s.
400 The increase in *C. purpureus* $\Delta^{13}\text{C}$ reflects drying conditions over time (Clarke *et al.*, 2012),
401 an effect also measured spatially across the bryophyte-dominated community of the Windmill
402 Islands. Here, moss gametophyte organic matter $\delta^{13}\text{C}$ values were significantly less negative
403 than in the dry, lichen-dominated community, which was suggested to indicate more frequent
404 submergence and consequently more significant diffusion limitation (Wasley *et al.*, 2012).

405

406 Without roots and with limited conduction systems, mosses are dependent on
407 precipitation, dewfall or ground water for hydration and the isotopic composition of this
408 source water ($\delta^{18}\text{O}_\text{SW}$) is an important determinant of cellulose isotope composition ($\delta^{18}\text{O}_\text{C}$).
409 Globally, the composition of source water depends on various factors, the most relevant for

410 Antarctica being the form and amount of precipitation. Following initial evaporation from
411 seawater (generating water vapour isotopically depleted in ^{18}O) successive precipitation
412 events (which favour the remaining heavy isotopes) become progressively depleted due to a
413 Rayleigh distillation (Gat, 2000). Snow (and subsequent snow melt water) is more
414 isotopically depleted than rain, and precipitation is also more depleted at high latitudes.
415 However, even if the water source is known, $\delta^{18}\text{O}_{\text{SW}}$ is often unequal to the isotopic
416 composition of leaf water ($\delta^{18}\text{O}_{\text{L}}$) at the site of cellulose synthesis due to preferential
417 evaporation of lighter water isotopologues (H_2^{16}O). Additionally, under high humidity
418 conditions the rate of diffusive vapour exchange may be sufficient to imprint $\delta^{18}\text{O}_{\text{L}}$ with the
419 atmospheric vapour isotope signal rather in place of $\delta^{18}\text{O}_{\text{SW}}$ (Helliker & Griffiths, 2007).
420 Furthermore, there is an approximately 27‰ biochemical fractionation during the synthesis
421 of organic matter, either following direct transfer of the $\delta^{18}\text{O}_{\text{L}}$ signal to sugars formed during
422 photosynthesis and thence to organic material, or after re-equilibration of carbonyl groups
423 that exchange with oxygen atoms in the surrounding water during the metabolic pathway of
424 incorporation into storage polysaccharides (Barbour, 2007, Da Silveira *et al.*, 1989, DeNiro
425 & Epstein, 1979, Sternberg *et al.*, 2006). The biochemical fractionation factor may be
426 temperature dependent, with particular sensitivity at low temperatures (5-15°C) (Sternberg &
427 Ellsworth, 2011) which would be highly relevant to Antarctic plants.

428 Thus, there are multiple factors that influence the measured oxygen isotope composition of
429 bryophyte material at any particular time or place, with further complexity introduced from
430 morphological and physiological differences between species. Factors which affect
431 desiccation tolerance, the timing of cellulose synthesis relative to the extent of saturation, and
432 microclimate and micro-topographical effects on relative humidity around the leaf could all
433 affect the extent of evaporative enrichment. On Signy Island, there was a consistent offset in
434 the oxygen isotope composition of cellulose between material obtained from low lying

435 hummocks, and more extensive moss banks (Royles *et al.*, 2013c). This was attributed to the
436 dominant water source in the former being more depleted snow melt water as compared to
437 summer precipitation.

438 The extent of capillary water is an important determinant of both the carbon and
439 oxygen isotope compositions, but $\delta^{18}\text{O}_C$ is less dependent upon the photosynthetic rate than
440 $\delta^{13}\text{C}_C$ where, in combination with the capillary water, photosynthetic rate largely determines
441 the diffusive supply of CO_2 from the atmosphere to the chloroplast (Rice & Giles, 1996,
442 Royles *et al.*, 2013b, Williams & Flanagan, 1996). The oxygen signal is largely dependent
443 upon the difference in relative humidity between the moss tissue and atmosphere. The two
444 isotope signals also represent subtly different time points. Whilst the $\delta^{13}\text{C}_C$ signal represents
445 atmospheric CO_2 the external water layer thickness and internal conductance during carbon
446 assimilation, $\delta^{18}\text{O}_C$ reflects the time of cellulose synthesis, when most oxygen atoms will
447 exchange and re-equilibrate with contemporary tissue water. Experimental evidence from the
448 desiccation tolerant moss *S. ruralis* suggests that this temporal separation may be important,
449 with $\delta^{13}\text{C}_C$ reflecting the time of maximum assimilation, just prior to metabolic limitation due
450 to desiccation, whilst cellulose synthesis occurs following re-saturation with source water
451 after rain / dewfall (Royles *et al.*, 2013b) as turgor pressure is required for cell wall expansion
452 and growth (S. A. Robinson pers. comm.). For moss banks and hummocks that experience
453 lower daily fluctuations in water content than *Syntrichia ruralis*, the separation between
454 periods of maximum assimilation and maximum cellulose synthesis are likely to be less
455 distinct. Further experimentation under controlled environmental conditions is required to
456 define these responses more generally.

457 With multiple factors influencing the measured $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, here we
458 consider the values in tandem, in an attempt to identify biologically relevant clusters (Figure
459 7). Measurements of $\delta^{13}\text{C}_C$ and $\delta^{18}\text{O}_C$ have been made on *C. aciphyllum* and *P. strictum* from

460 extensive moss banks and hummocks on Signy Island, and from a hummock at Lazarev Bay
 461 on Alexander Island (Figure 7) (Royles *et al.*, 2013a, Royles *et al.*, 2012, Royles *et al.*,
 462 2013c). $\Delta^{13}\text{C}_\text{C}$ values were used to remove the impact of the systematic isotopic depletion in
 463 atmospheric CO_2 over the industrialised period; however, a source effect was not removed
 464 from $\delta^{18}\text{O}_\text{C}$, as there was no independent record of source water composition. When both
 465 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements are considered the data points separate into three clusters:

- 466 1) *C. aciphyllum* from extensive Signy Island banks ($\Delta^{13}\text{C} = 14\text{-}17\text{‰}$, $\delta^{18}\text{O} = 26\text{-}31\text{‰}$)
- 467 2) *C. aciphyllum* from small Signy Island hummocks ($\Delta^{13}\text{C} = 15\text{-}17\text{‰}$, $\delta^{18}\text{O} = 22\text{-}27\text{‰}$)
- 468 3) *P. strictum* from Signy Island and Lazarev Bay ($\Delta^{13}\text{C} 17\text{-}19.5\text{‰}$, $\delta^{18}\text{O} = 23\text{-}27\text{‰}$)

469 This can also be characterised as:

- 470 1) *C. aciphyllum*: $\Delta^{13}\text{C} < 17\text{‰}$;
 471 *P. strictum*: $\Delta^{13}\text{C} > 17\text{‰}$
- 472 2) Hummock (e.g. Fig. 2f): $\delta^{18}\text{O} < 26\text{‰}$;
 473 Bank (e.g. Fig. 2a): $\delta^{18}\text{O} > 27\text{‰}$

474 Several factors underlie these groupings. Species has a dominant effect on $\Delta^{13}\text{C}$. Lamellae on
 475 the leaves of *P. strictum* facilitate relatively faster diffusion of CO_2 into the leaf as compared
 476 to *C. aciphyllum* under the same moisture conditions, hence the higher discrimination.
 477 *Chorisodontium aciphyllum* is dominant in wetter areas whilst *P. strictum* is associated with
 478 drier conditions, (Fenton & Smith, 1982), as, being endohydric, *P. strictum* has some
 479 capacity for internal water transport which enables tissues to maintain hydration for longer in
 480 dry conditions. It is surprising not to see a latitude effect in *P. strictum* $\delta^{18}\text{O}$ values, as being
 481 9° further south than Signy Island, the isotopic composition of precipitation at Lazarev Bay
 482 would be expected to be more depleted in ^{18}O values. In contrast, whilst the carbon isotope
 483 composition of all the *C. aciphyllum* samples falls within the 14-17‰ range, the oxygen
 484 isotope composition of cellulose from bank-forming *C. aciphyllum* is significantly higher

485 than that from hummock forming *C. aciphyllum*. This offset can be attributed to the inputs of
486 isotopically lighter summer precipitation, as compared to more depleted melt water, and also
487 influenced by the extent of evaporative enrichment (Royles *et al.*, 2013c).

488 Variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements of 3‰ and 4‰ respectively remains within the
489 clusters, and indeed individual cores, representing variation measured over time that reflects
490 local environmental changes. Photosynthetic conditions can vary locally, as cryo-perturbation
491 makes the moss surface uneven at the centimetre scale, with the tops of ridges being driest
492 and windiest (Lovelock & Robinson, 2002, Lucieer *et al.*, 2013). This can affect both $\Delta^{13}\text{C}$
493 and $\delta^{18}\text{O}$ measurements, with higher $\Delta^{13}\text{C}$ values associated with drier conditions and higher
494 $\delta^{18}\text{O}$ with a greater degree of evaporative enrichment. On the millennial scale that the *C.*
495 *aciphyllum* core data represents, differential rates of growth and the disturbing effects of
496 winter snow cover may alter the relative positioning of the growing moss within the local
497 micro-topography. Thus, the stable isotopic composition of mosses over time is dependent
498 upon species and can provide information about the growth form and microclimate conditions
499 at the leaf surface, as well as reflecting to some extent the narrow range of environmental
500 conditions which support growth.

501

502 Not all isotopic variation can currently be attributed to a particular environmental factor,
503 hence more laboratory work is required to elucidate under controlled conditions some of the
504 drivers of the variation (such as the influence of temperature on isotope fractionation factors
505 during cellulose biosynthesis (Sternberg & Ellsworth, 2011)) and also additional proxies
506 could be analysed to provide more information about the past. For example, the analysis of
507 $\delta^2\text{H}_\text{C}$, alongside ^{18}O isotopomers, could be used to compare the $\delta^2\text{H}$ –temperature relationship
508 along modern elevation and latitude gradients. In this way, *Sphagnum* $\delta^2\text{H}_\text{C}$ from a
509 Patagonian peat bog was used to reconstruct the past meteoric water composition and

510 revealed abrupt temperature changes during the late Pleistocene and early and middle
511 Holocene (Pendall *et al.*, 2001). By combining $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values from organic compounds
512 it is possible to estimate the meteoric water composition at the time of synthesis, and
513 potentially estimate temperature and relative humidity conditions that could result in the
514 measured isotope values (Edwards, 1993, Edwards *et al.*, 2000).

515

516 **5. Contemporary moss physiology: integrating isotope signals, plant**
517 **water relations, photosynthetic gas exchange and chlorophyll**
518 **fluorescence**

519 Identifying conditions under which mosses are photosynthetically active, and especially
520 periods of net assimilation, is crucial to interpreting preserved proxy signals and predicting
521 the responses of moss to climate changes. In addition to water availability, which is the most
522 critical factor in determining Antarctic moss distribution (Cannone *et al.*, 2013, Colesie *et al.*,
523 2014, Convey *et al.*, 2014), diffusion limitation, life-form, length of growing season (Royles
524 *et al.* 2012) and light availability (Loisel *et al.* 2012; Charman *et al.* 2013) have also been
525 implicated as major contributors to the dynamics of moss growth at the ecosystem level.

526

527 Photosynthetic light use can be estimated using chlorophyll fluorescence as a non-destructive
528 measure of photosystem activity, allowing quantum yield (Ψ_{PSII}), electron transport rate
529 (ETR) and energy dissipation (non-photochemical quenching, NPQ) to be determined for
530 Antarctic mosses under laboratory (Stanton *et al.*, 2014) and field conditions (Robinson *et al.*,
531 2000, Schlensoeg *et al.*, 2013) to show, for example, the relative sensitivity of mosses to
532 desiccation (Robinson *et al.*, 2000). The mesic mosses *Bryum argenteum* and *B.*
533 *pseudotriquetrum* had sufficient water for continuous metabolism with seasonally integrated

534 ETR (representing assimilation) largely dependent upon light and temperature (Schlensog *et*
535 *al.*, 2013). In contrast, the most xeric mosses (*C. purpureus*, *Stereocaulon alpinum* and
536 *Andreaea gainii*) were only active for 40-50% of time. With 60% activation *Polytrichum*
537 *alpinum* was the most active xeric moss as being endohydric it has as some capacity for water
538 transport and a cuticle to reduce the rate of water loss (Schlensog *et al.*, 2013).

539

540 By following photosynthetic gas exchange and isotope discrimination during a drying curve
541 stable isotope physiology and hydrology can be investigated (Rice & Giles, 1996, Royles *et*
542 *al.*, 2013b, Williams & Flanagan, 1996). Chlorophyll fluorescence and derived
543 characteristics (ETR, NPQ) can also be used to track photosynthetic activity and the impact
544 of dehydration (Figure 8, J Royles, H Jenkins and H Griffiths, unpublished data). During
545 desiccation, *S. ruralis* ETR increased as photosynthesis became less diffusion limited,
546 reaching a maximum at a relative water content (RWC) of 150%; below 100% RWC, ETR
547 declined rapidly as moss photosynthesis was compromised by desiccation (Figure 8a). This
548 profile tracked the real-time carbon isotope discrimination signal (Royles *et al.*, 2013b) and
549 was consistent with ETR as an additional proxy for carbon uptake. Successive light response
550 curves throughout the drying curve (Figure 8b) also show the overall responsiveness of
551 fluorescence, and potential for the development of ETR as a remotely-sensed proxy for
552 photosynthetic activity as a function of moss hydration status. Additional measurements on
553 this system showed that the isotope composition of soluble carbohydrates can also be used to
554 integrate daily carbon gain. The ^{13}C signal ($\Delta^{13}\text{C}=20\pm 0.5\text{‰}$ (n=8)) was indicative of optimal
555 gas exchange, whilst the ^{18}O signal was more sensitive to evaporative enrichment during
556 desiccation (increasing from $21.7\pm 0.8\text{‰}$ to $25.1\pm 0.6\text{‰}$ (n=4 each)) as it was probably re-
557 equilibrating with tissue water during growth in the light (J Royles, A Sturgess and H
558 Griffiths, unpublished data). The rapid physiological responses of *S. ruralis* to RWC reflect

559 the tight coupling between the moss and current environmental conditions. We would expect
560 bank forming mosses, with less variable tissue water contents, to show somewhat buffered, or
561 muted, coupling between changing environmental conditions, fluorescence and isotope
562 signals. However, the prospects for resolving the variations within and between ^{13}C and ^{18}O
563 signals in Antarctic mosses seem promising (Figure 7), as well as the use of chlorophyll
564 fluorescence to investigate moss bank responses at ecosystem and regional scales.

565

566 **6. Responses of polar mosses to climate change**

567 There are many urgent ecological and environmental problems in the Arctic related to mosses
568 in a changing climate, but the geographical range of species and life-forms are difficult to
569 track individually. The goal was to translate what we have learned from more simple systems
570 in Antarctica, and apply to Arctic habitats.

571 *i) Direct and indirect responses to temperature*

572 For Antarctic bryophytes, chlorophyll fluorescence measurements were used to infer that the
573 extent of the hydrated (active) period was a more important influence on photosynthetic
574 performance than temperature, with reliance on melt water or more temporary activation
575 from precipitation being a key factor (Schlensog *et al.*, 2013). Increases in temperature will
576 alter water availability to mosses through changes in the timing and extent of melt streams
577 and increases in active layer depth (Guglielmin *et al.*, 2014). The speed with which plants
578 reactivate photosynthesis following both prolonged winter freezing, rapid freeze-thaw cycles
579 and periods of summer desiccation, is relevant to the seasonal assimilates preserved in
580 organic matter. Mesic Antarctic mosses take 24 h to fully recover net photosynthesis
581 following desiccation due to resaturation respiration (Schlensog *et al.*, 2004), a transient
582 increase in respiration widely seen in anhydrobiotic organisms following rewetting, possibly
583 due to metabolic costs of repair, or mitochondrial inefficiency (Nijp *et al.*, 2014).

584 Experimental warming was tentatively associated with a decrease in moss cover in the Arctic
585 tundra, but the response varied substantially over space and time (Elmendorf *et al.*, 2012) and
586 with limited samples it is difficult to account for the influence of ambient conditions and
587 species-specific dynamics (Lang *et al.*, 2012, Street *et al.*, 2013) especially as moss
588 distribution may be more sensitive to moisture availability than warming (Lang *et al.*, 2009).

589 Other indirect effects likely to be associated with a warming climate for both polar regions
590 include the extended growing season identified for maritime (Royles *et al.*, 2012) and
591 continental Antarctic mosses (Clarke *et al.*, 2012), as well as altered precipitation patterns
592 affecting wetting and light limitation (cloudiness). In conclusion, it is predicted that
593 significant changes will occur to both polar plant growth and vegetation distribution in
594 response to a changing climate (Chapin III, 2003, Chapin III *et al.*, 2005, Chapin III *et al.*,
595 2010), but a more detailed understating of how contrasting plant functional groups respond to
596 these challenges (Turetsky *et al.*, 2012) is needed to test predictions of polar ecosystem
597 resilience to climate change.

598 ***ii) Direct and indirect responses to light***

599 Bryophyte photosynthetic activity is responsive to light intensity in moist habitats, but less so
600 in more xeric habitats, where water limitation is the major determinant (Schlensog *et al.*,
601 2013). Changes to cloud cover will alter light availability for photosynthesis, at Vernadsky
602 station (Fig 1a) cloud cover increased significantly between 1960 and 2005 (Kirchgaßner,
603 2010). The growth of *Sphagnum* was directly related to light intensity in wetter sites in
604 Alaska, where increasing water table and acidification were associated with a decline in black
605 spruce (Fenton & Bergeron, 2006). In two recent extensive meta-analyses of peat
606 accumulation, light availability was related to *Sphagnum* growth, particularly at high latitudes
607 (Charman *et al.*, 2013, Loisel *et al.*, 2012). Indeed, total carbon accumulation in northern

608 peatlands over the past 1000 y was linearly related to photosynthetically active radiation
609 projected over the growing season (defined as the Growth Degree Days, for which air
610 temperature is greater than 0°C, GDD0), and with a stronger correlation than with GDD0
611 alone (Charman *et al.*, 2013).

612 *iii) Responses to water availability*

613 Mosses from xeric habitats will go through multiple desiccation cycles during a growing
614 season and be tolerant of desiccation (c.f. “low-inertia” species (Proctor & Tuba, 2002)),
615 whilst those in wet flushes are likely to remain damp and make more use of dehydration
616 repair processes (“high-inertia species” (Proctor & Tuba, 2002)) (Proctor, 2000, Schlenso *et al.*,
617 2004). Furthermore, carbon use efficiency differs between species that maintain a
618 relatively constant RWC over time (e.g. *Sphagnum* spp.) and those which are metabolically
619 active throughout drying cycles from saturation to desiccation (Street *et al.*, 2013). The
620 biphasic response of carbon accumulation to Precipitation/Evaporation (P/E) over the past
621 1000 y, identified by both (Charman *et al.*, 2013, Loisel *et al.*, 2012), is consistent with daily
622 changes seen in individual mosses (Royles *et al.*, 2013b) (Figure 8a). Thus, there is an
623 optimal carbon accumulation under relatively low P/E values, with a rapid decline in growth
624 under driest conditions (high evaporative demand), and a more gradual reduction under
625 increasingly wet conditions (higher P/E conditions (see Figure 5c in (Charman *et al.*, 2013)).
626 Therefore, there is still a need to characterise the relationships between light availability and
627 the impact of warmer and wetter, or warmer and drier, conditions for bryophyte
628 photosynthetic activity over the course of a longer growing season.

629 An important additional consideration for the water relations of mosses is plant life-form and
630 functional type (filamentous, hummock/hollow (Turetsky *et al.*, 2012)). There may be
631 separation between the photosynthetic tissues, which are usually restricted to the top 5 mm of

632 shoots and thus exposed to wind and hence dry out quickly, and water storage in spongy
633 tissue below (Stanton *et al.*, 2014). Rates at which individual shoots lose water to the
634 atmosphere can be very different to that of whole clumps and capacity for internal water
635 redistribution is a critical component of physiology. Similarly, the moss temperature can be
636 much warmer than the air temperature (Longton, 1982, Smith, 1988b), and it is important to
637 separate the effects of vapour pressure differences between tissue and atmosphere (VPD) and
638 air temperature: VPD, which determines the rate of drying, varies non-linearly with
639 temperature (Stanton *et al.*, 2014). Indeed, polar mosses can have high rates of
640 photosynthesis over a range of temperatures (Davey & Rothery, 1997, Pannowitz *et al.*,
641 2005). The strong influence of VPD on moss photosynthesis in both *C. purpureus* and *S.*
642 *antarctici* means that temperature, precipitation and VPD all need to be modelled accurately
643 before conclusions can be drawn about the effects of climate change (Stanton *et al.*, 2014).

644

645 **7. Scaling physiological proxies to monitor and model climate change**

646 **for the future**

647 Mosses from across Antarctica are responding to climate change with changes in growth rates
648 and stable isotope proxies as discussed above (Clarke *et al.*, 2012, as discussed above; Royles
649 *et al.*, 2013a, Wasley *et al.*, 2012). However, whilst data are logistically difficult to obtain in
650 such remote regions, interpretation might be relatively simple compared to complex seasonal
651 vegetation-permafrost dynamics in Arctic ecosystems (Chapin III *et al.*, 2010, Sistla *et al.*,
652 2013, Tingley & Huybers, 2013, Turetsky *et al.*, 2012).

653 Firstly, one must distinguish between boreal forest (coniferous dominated, mainly north of
654 45°N) and tundra (8.2 M km², mostly north of 65°N) (Xu *et al.*, 2013), and the contrasting
655 responses of bryophytes and their associated carbon storage capacity (Charman *et al.*, 2013,
656 Sistla *et al.*, 2013, Yu *et al.*, 2010). Within this enormous range of habitats, three generalised

657 responses might be anticipated: (i) a northerly shift in vegetation boundaries associated with
658 rapid warming and restricted extent of permafrost (Baltzer *et al.*, 2014, Turetsky *et al.*, 2012,
659 Turetsky *et al.*, 2010, Xu *et al.*, 2013); (ii) increasing frequency and intensity of drought, and
660 associated fires in more continental areas, likely to reduce *Sphagnum* dominance and increase
661 conifers capable of regenerating after fire (Chapin III, 2003, Chapin III *et al.*, 2010, Turetsky
662 *et al.*, 2012, Turetsky *et al.*, 2010); (iii) increased precipitation in more maritime regions of
663 Alaska and western Canada, as well as in Fennoscandinavia and Western Siberia, leading to
664 enhanced *Sphagnum* growth, elevated water tables and forest decline associated with
665 paludification (Crawford, 2008, Crawford *et al.*, 2003, Fenton & Bergeron, 2006, Turetsky *et*
666 *al.*, 2012).

667 Key questions for the future relate to the development of methods and approaches needed to
668 monitor these processes remotely, to allow modelling and predictions of climate change
669 impacts to be validated (Chapin III *et al.*, 2010, Crawford *et al.*, 2003). In the Antarctic, we
670 have recently seen the use of Landsat satellite images to project current vegetation
671 distribution via Normalised Distribution Vegetation Index (NDVI: (Fretwell *et al.*, 2011))
672 and spatial variations in moss bank surface temperature and spectral reflectance, estimated
673 from an Unmanned Aerial Vehicle (UAV), mounted with sensors and cameras (Turner *et al.*,
674 2014). Chlorophyll fluorescence has been used to ground-truth the responses of cryptogamic
675 communities to water availability (Schlensog *et al.*, 2013), and there is now the possibility of
676 using the Laser Induced Fluorescence Technology (LIFT) as a remote-sensing system, across
677 a range of spatial scales (Kolber *et al.*, 2005, Pieruschka *et al.*, 2012). Finally, the
678 interpretation of solar-induced fluorescence from UAVs (Damm *et al.*, 2014) or satellite
679 systems (Zhang *et al.*, 2014) has recently been provided with a quantitative framework to
680 interpret components such as quantum yield, ETR and NPQ (Guanter *et al.*, 2014). The
681 opportunity for their use in distinguishing moss photosynthetic activity and carbon

682 sequestration as a function of water availability, across a changing forest mosaic, and at
683 regional scales for polar regions, is now a realistic prospect. There will be exciting
684 opportunities for ground-truthing these remote proxies under challenging Arctic and
685 Antarctic conditions.

686 **8. Conclusion**

687 In conclusion, recent key analytical and modelling advances in the use of stable isotopes of
688 carbon have helped to provide a quantitative basis to moss photosynthesis, growth and
689 seasonality across Antarctica, and with implications for arctic and boreal regions. Many of
690 the eight factors identified by Fenton and Smith (1982) as being important for moss
691 establishment in Antarctica, are sensitive to a changing climate, including length of growing
692 season, reduction in permanent snow cover, substrate stability (extent of permafrost), wind
693 speed, nutrient availability and water supply. Such conditions already partly explain the
694 contrasting degree of moss colonisation between maritime and continental Antarctica, and the
695 increased extent of moss bank formation in the Scotia Arc. Having reviewed the rates of moss
696 bank growth in these habitats, we have also demonstrated the power of stable isotopes (^{13}C ,
697 ^{18}O) to integrate photosynthesis, growth and water sources. However, more work is needed to
698 understand the biochemical and hydraulic determinants of oxygen and deuterium signals, and
699 their relationship to climatic inputs. Photosystem II fluorescence was demonstrated to be one
700 potential physiological proxy which integrates the effect of light intensity,
701 precipitation/evaporation rates on photosynthetic activity and hence bryophyte growth and
702 carbon sequestration. Once validated by ground truthing, solar-induced fluorescence, sensed
703 remotely by UAVs or satellites, could be used to map bryophyte productivity in polar and
704 boreal regions. For the arctic, it should be possible to capture the changing spatial landscape,
705 as paludification in warming, maritime areas and increased intensity of fires in continental

706 regions, are anticipated in the future. Additionally, the integration of surface proxies and a
707 better understanding of stable isotope signals will also improve the historical reconstruction
708 of climatic conditions for peat archives, as both temporal and spatial proxies will be needed
709 to understand how polar-regions will respond to warming and other climate change effects.

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714

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1085 **Figure Legends**

1086 Figure 1 a) Mean growing season temperatures (November-March) over fifty years at
1087 meteorological stations around Antarctica (SCAR, 2014). Box encompasses maritime
1088 Antarctic (M), remainder is continental Antarctica (C); b) Major sites of moss peat banks and
1089 the associated oldest basal dates. At Signy Island (Fenton, 1982), Elephant Island (Björck *et*
1090 *al.*, 1991b), Norsel Point and Lazarev Bay (Convey *et al.*, 2000, Royles *et al.*, 2013a) the
1091 growth is continuous and consists of *Chorisodontium aciphyllum* and/or *Polytrichum*
1092 *strictum*. Norsel Point sample processed following same methods as (Royles *et al.*, 2012). All
1093 dates re-calibrated from published ¹⁴C ages using Caib (v. 7.0.2) (Stuiver & Reimer, 1993)
1094 and the SHCal13 dataset (Hogg *et al.*, 2013). Dates presented are the median probability
1095 years, with associated 2 σ ranges in brackets.

1096 Figure 2: a) Signy Island *Chorisodontium aciphyllum* moss peat bank; b) Cross section
1097 through top of *C. aciphyllum* core showing individual moss stems aligned below 5 mm of
1098 green photosynthetic tissue (scale bar represents 5 cm); c) Ridged surface of *C. aciphyllum*
1099 moss bank with moribund areas and epilithic lichens (scale bar represents 10 cm; d) Signy
1100 Island *C. aciphyllum* moss peat bank; e) Cross-section through deep *C. aciphyllum* peat; f)
1101 Signy Island *C. aciphyllum* hummock.

1102

1103 Figure 3: Age-depth models developed from bomb-spike dating of moss growth from the
1104 Windmill Islands (*Ceratodon purpureus*, 3 blue lines) and Vestfold Hills (*Bryum*
1105 *pseudotriquetrum* and *Bryoerythrophyllum recurvirostre*, 2 purple lines) (Clarke *et al.*, 2012)
1106 in continental Antarctica (C) and from the maritime Antarctic (M) *Chorisodontium*
1107 *aciphyllum* from Signy Island (green line) (Royles *et al.*, 2012) and *Polytrichum strictum*
1108 from Lazarev Bay (red line) (Royles *et al.*, 2013a).

1109

1110 Figure 4: Peat accumulation rate over time on Signy Island and at Lazarev Bay (Royles *et al.*,
1111 2013a). Calculated from bulk density measurements and age depth model, smoothed over
1112 three successive time-points, this takes into account the increasing effect of compression as
1113 the accumulations become deeper.

1114

1115 Figure 5a): Measured $\delta^{13}\text{C}$ of *Ceratodon purpureus* (3 blue lines) organic matter from
1116 continental (C) Antarctica (Clarke *et al.*, 2012). In the maritime Antarctic (M) at Lazarev Bay
1117 (red) (Royles *et al.*, 2013a) and Signy Island (green) (Royles *et al.*, 2012) $\delta^{13}\text{C}$ was measured
1118 in cellulose. Comparative measurements of organic matter and cellulose showed a highly
1119 significant linear relationship between $\delta^{13}\text{C}_{\text{OM}}$ and $\delta^{13}\text{C}_{\text{C}}$ ($R^2=0.73$, $p<0.0001$, $n=40$, $F=108$,
1120 $y=0.75x - 4.58$) from which $\delta^{13}\text{C}_{\text{OM}}$ were derived; b) Source-independent discrimination
1121 ($\Delta^{13}\text{C}$) was calculated for each measurement (see text for details; NB. Different y-axis
1122 scales).

1123

1124 Figure 6a) Measured carbon isotope composition of cellulose ($\delta^{13}\text{C}_{\text{C}}$) and b) Source
1125 independent discrimination ($\Delta^{13}\text{C}$; see text for details) over time from Signy Island
1126 *Chorisodontium aciphyllum* (3 green lines) (Royles *et al.*, 2012) and Lazarev Bay
1127 *Polytrichum strictum* (red) (Royles *et al.*, 2013a).

1128

1129 Figure 7: Extent of source independent carbon ($\Delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope
1130 discriminations measured in cellulose for Signy Island *Chorisodontium aciphyllum* growing
1131 in large banks (green diamonds, orange circles) and a small hummock (blue upward triangle).

1132 In addition, *Polytrichum strictum* hummocks from Signy Island (Red down triangles) and
1133 Lazarev Bay (purple squares). $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measured on separate sub-samples of cellulose
1134 as described in (Royles *et al.*, 2013a, Royles *et al.*, 2012, Royles *et al.*, 2013c). Arrows
1135 represent direction and hypothetical mechanisms for isotopic variation.

1136 Figure 8: Desiccation response of *Syntrichia ruralis*: a) Max electron transport rate (ETR) as
1137 a function of relative water content (RWC). Error bars: 1 SE (n=4); b) Light response curves
1138 for desiccating *Syntrichia ruralis*: mean ETR as a function of light intensity. Six successive
1139 curves were measured as the tissue RWC declined from 350% (line 1, red) through to 50%
1140 (purple, line 6). Equivalent RWC (1-6) marked on (a) (n=4, dashed lines=SE)

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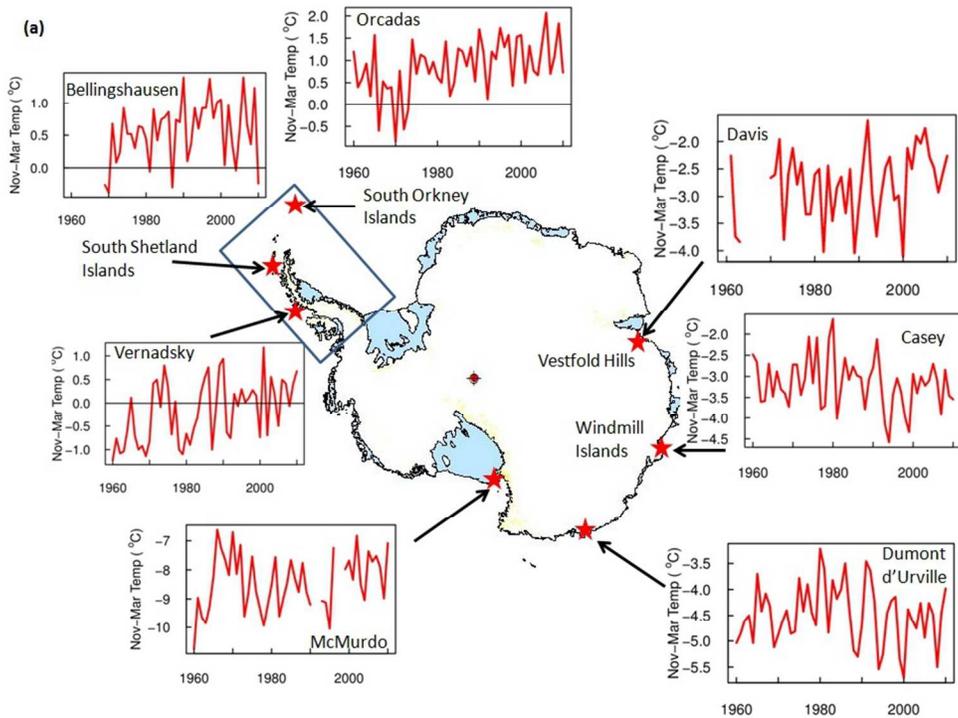


Figure 1a) Map of Antarctica and summer temperature trends
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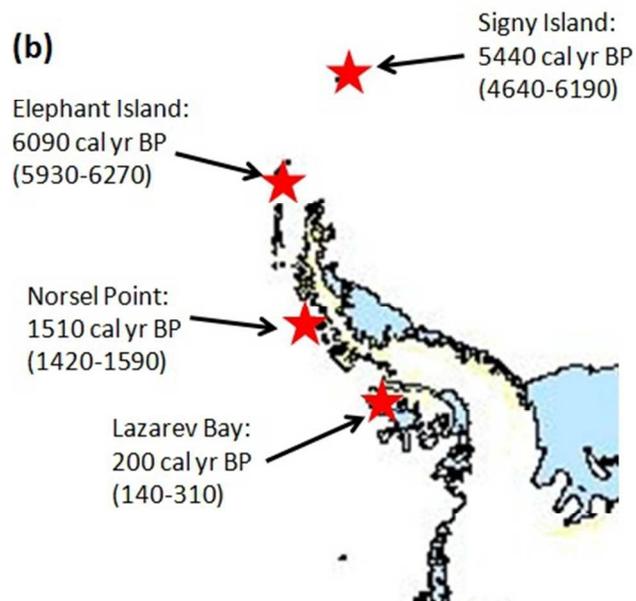


Figure 1b) Basal age of maritime Antarctic peat banks
179x112mm (96 x 96 DPI)

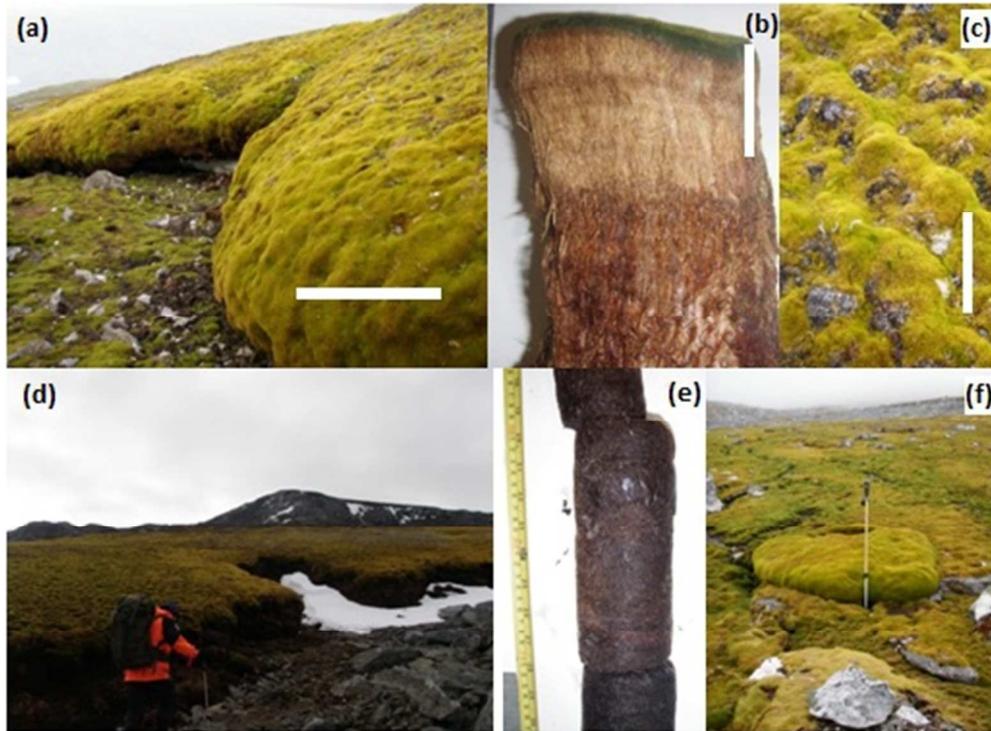


Figure 2 a) Signy Island *Chorisodontium aciphyllum* moss peat bank; b) Cross section through top of *C. aciphyllum* core showing individual moss stems aligned below 5 mm of green photosynthetic tissue (scale bar represents 5 cm); c) Ridged surface of *C. aciphyllum* moss bank with moribund areas and epilithic lichens (scale bar represents 10 cm); d) Signy Island *C. aciphyllum* moss peat bank; e) Cross-section through deep *C. aciphyllum* peat; f) Signy Island *C. aciphyllum* hummock .
136x100mm (96 x 96 DPI)

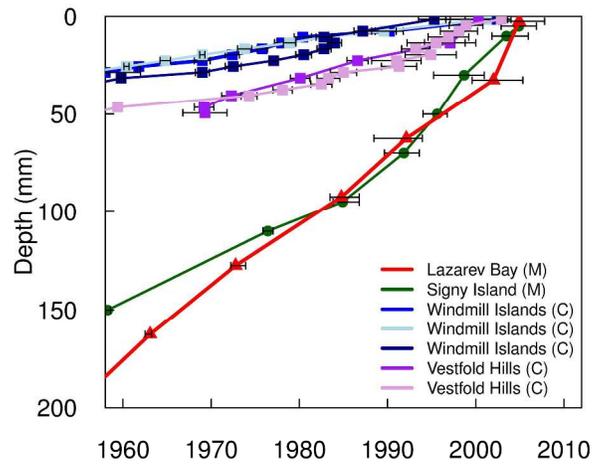


Figure 3) Age-depth models developed from bomb-spike dating of moss growth from the Windmill Islands (*Ceratodon purpureus*, 3 blue lines) and Vestfold Hills (*Bryum pseudotriquetrum* and *Bryoerythrophyllum recurvirostre*, 2 purple lines) (Clarke et al., 2012) in continental Antarctica (C) and from the maritime Antarctic (M) *Chorisodontium aciphyllum* from Signy Island (green line) (Royles et al., 2012) and *Polytrichum strictum* from Lazarev Bay (red line) (Royles et al., 2013a).
279x361mm (300 x 300 DPI)

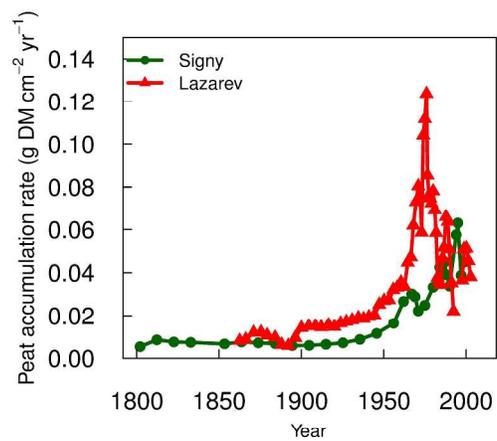


Figure 4) Peat accumulation rate over time on Signy Island and at Lazarev Bay (Royles et al., 2013a). Calculated from bulk density measurements and age depth model, smoothed over three successive time-points, this takes into account the increasing effect of compression as the accumulations become deeper.
279x361mm (300 x 300 DPI)

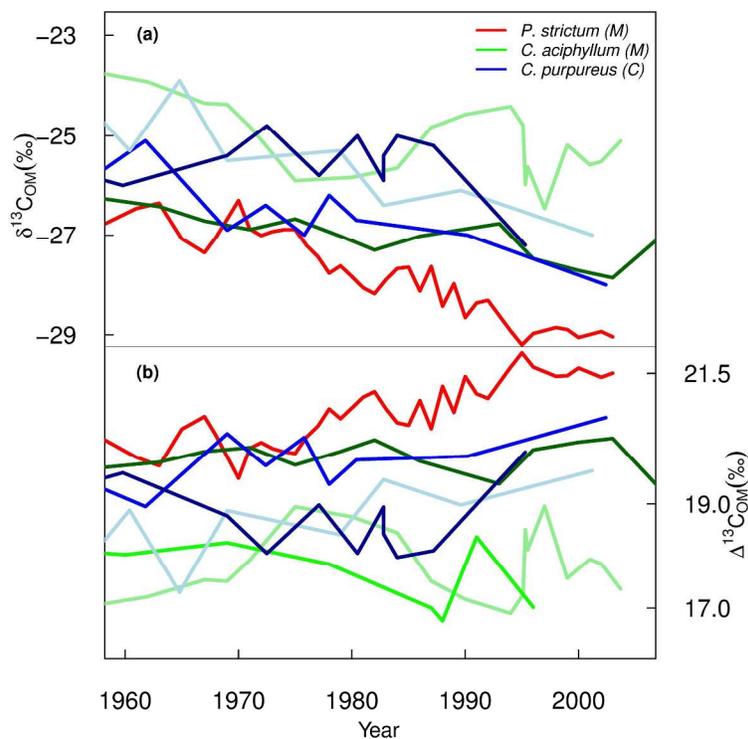


Figure 5a): Measured $\delta^{13}\text{C}$ of *Ceratodon purpureus* (3 blue lines) organic matter from continental (C) Antarctica (Clarke et al., 2012). In the maritime Antarctic (M) at Lazarev Bay (red) (Royles et al., 2013a) and Signy Island (green) (Royles et al., 2012) $\delta^{13}\text{C}$ was measured in cellulose. Comparative measurements of organic matter and cellulose showed a highly significant linear relationship between $\delta^{13}\text{C}_{\text{COM}}$ and $\delta^{13}\text{C}_{\text{CC}}$ ($R^2=0.73$, $p<0.0001$, $n=40$, $F=108$, $y=0.75x - 4.58$) from which $\delta^{13}\text{C}_{\text{COM}}$ were derived; b) Source-independent discrimination ($\Delta^{13}\text{C}$) was calculated for each measurement (see text for details; NB. Different y-axis scales).
279x361mm (300 x 300 DPI)

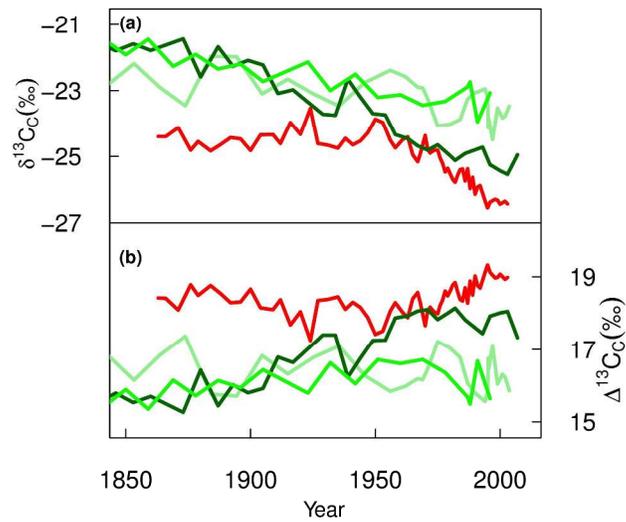


Figure 6a) Measured carbon isotope composition of cellulose ($\delta^{13}C_C$) and b) Source independent discrimination ($\Delta^{13}C_C$; see text for details) over time from Signy Island *Chorisodontium aciphyllum* (3 green lines) (Royles et al., 2012) and Lazarev Bay *Polytrichum strictum* (red) (Royles et al., 2013a).
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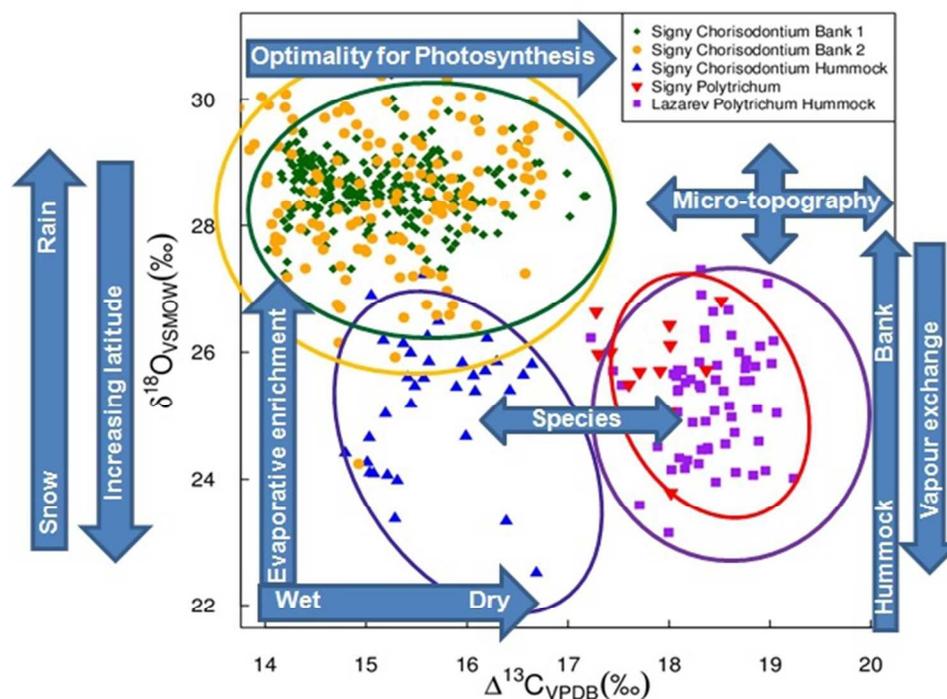


Figure 7: Extent of source independent carbon ($\Delta^{13}C$) and oxygen ($\delta^{18}O$) isotope discriminations measured in cellulose for Signy Island Chorisdontium aciphyllum growing in large banks (green diamonds, orange circles) and a small hummock (blue upward triangle). In addition, Polytrichum strictum hummocks from Signy Island (Red down triangles) and Lazarev Bay (purple squares). $\delta^{13}C$ and $\delta^{18}O$ measured on separate sub-samples of cellulose as described in (Royles et al., 2013a, Royles et al., 2012, Royles et al., 2013c).

Arrows represent direction and hypothetical mechanisms for isotopic variation.

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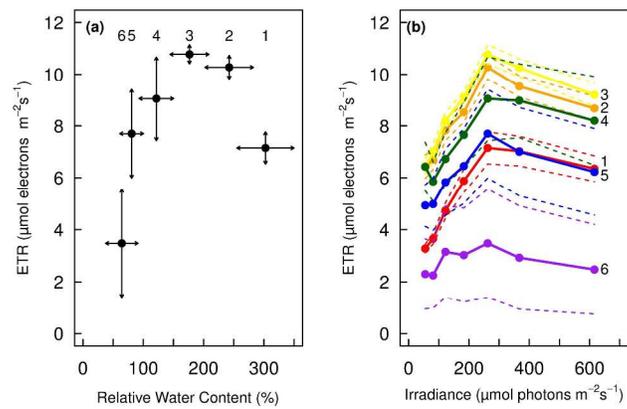


Figure 8: Desiccation response of *Syntrichia ruralis*: a) Max electron transport rate (ETR) as a function of relative water content (RWC). Error bars: 1 SE (n=4); b) Light response curves for desiccating *Syntrichia ruralis*: mean ETR as a function of light intensity. Six successive curves were measured as the tissue RWC declined from 350% (line 1, red) through to 50% (purple, line 6). Equivalent RWC (1-6) marked on (a) (n=4, dashed lines=SE)
279x361mm (300 x 300 DPI)