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

Running head: Lessons from Antarctic moss banks archives

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Abstract:

Mosses are the dominant plants in polar and boreal regions, areas which are experiencing rapid impacts of regional warming. Long-term monitoring programmes provide some records of the rate of recent climate change, but moss peat banks contain an unrivalled temporal record of past climate change in terrestrial plant Antarctic systems. We summarise the current understanding of climatic proxies and determinants of moss growth for contrasting continental and maritime Antarctic regions, as informed by \textsuperscript{13}C and \textsuperscript{18}O signals in organic material. Rates of moss accumulation are more than three times higher in the maritime Antarctic than continental Antarctica with growing season length being a critical determinant
of growth rate, and high carbon isotope discrimination values reflecting optimal hydration conditions. Correlation plots of $^{13}$C and $^{18}$O values show that species (*Chorisodontium aciphyllum* / *Polytrichum strictum*) and growth form (hummock / bank) are the major determinants of measured isotope ratios. The interplays between moss growth form, photosynthetic physiology, water status and isotope composition are compared with developments of secondary proxies, such as chlorophyll fluorescence. These approaches provide a framework to consider the potential impact of climate change on terrestrial Antarctic habitats as well as having implications for future studies of temperate, boreal and Arctic peatlands. There are many urgent ecological and environmental problems in the Arctic related to mosses in a changing climate, but the geographical ranges of species and life-forms are difficult to track individually. Our goal was to translate what we have learned from the more simple systems in Antarctica, for application to Arctic habitats.

1. Introduction

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

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

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

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

Both polar-regions experience low mean annual temperatures, seasonal extremes in day length and often have low free water availability. At high northern latitudes recent temperatures are unprecedented over at least the last 600 years (Tingley & Huybers, 2013),
and the maritime Antarctic Peninsula (AP), the most vegetated area of Antarctica, has been one of the most rapidly warming regions on Earth (Turner et al., 2009). As winter temperatures increase more rapidly than summer temperatures, polar seasonality has decreased (Franzke, 2012, Xu et al., 2013), and permafrost distribution has altered (Bockheim et al., 2013, Guglielmin et al., 2014, Quinton et al., 2011, Turetsky et al., 2007) which is expected to have significant effects on the global carbon budget (Koven et al., 2011, Schuur et al., 2009). Earlier annual melting of both northern (Surdu et al., 2014) and southern (Quayle et al., 2002) polar lakes indicates a potential lengthening of the biological growing season. Despite the similar physical responses of the poles to warming, the contrasting relative geographical isolation of Arctic and Antarctic terrestrial ecosystems have generated substantial differences in past, present and likely future floral diversity.

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

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

2. Distribution, past change and possible future dynamics of maritime Antarctic peat banks

The majority of high latitude Southern Hemisphere peatlands are in Patagonia, however they comprise only 1% of the global peatland area (Yu et al., 2010). Patagonian peatlands experience a climate with low precipitation and mild temperatures, and this minimal seasonality facilitates a long, potentially continuous, growing season (Loisel & Yu, 2013, Smith & Clymo, 1984). Peat addition rates are high, as conditions favour long periods of assimilatory carbon gain, whilst decomposition is limited by low summer temperatures (Loisel & Yu, 2013). Significant peat accumulations are also present on several sub-
Antarctic islands (Van der Putten et al., 2012), with this region again being characterised by limited seasonality in many environmental variables (Convey, 2013).

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

The appropriate interpretation of palaeoclimate archives in the context of broader spatial and temporal changes requires accurate methods for dating material. The purity and cryo-
protection of moss shoots, the absence of roots and minimal translocation of substances makes moss peat ideal material for accurate radiocarbon dating (Björck et al., 1991a). Dating of basal peat provides a minimum date at which conditions became suitable for net assimilation following the Last Glacial Maximum (LGM). The Antarctic moss banks vary in their age, accumulation rate and continuity, with the oldest known banks on Elephant Island (61°08’S 054°42’W) dating back over 5000 years (Björck et al., 1991b). The new date for the base of the peat at Norsel Point, Anvers Island (64°45’S 064°05’W), 620 km SW of Elephant Island suggests accumulation for at least 1500 years, whilst at the southernmost site, a further 600 km SSW on Alexander Island (69°22’S 71°51’W) the basal date shows that net accumulation began within the last two centuries (Figure 1b).

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

1. **Length of time the ground is snow-free in summer**

Moss requires snow and ice-free ground on which to establish, and, although limited photosynthesis can occur through some snow cover as long as the tissue has thawed (Longton, 1988), the majority of net assimilation will occur following the spring snow melt. The length of time that the ground is snow-free in summer has generally increased. On Signy Island, ice cover reduced by 45% between 1950 and 1990 (Smith, 1990), and freshwater lakes are annually ice-free for an additional two months (Quayle et al., 2002), both of which are proxies for an increase in the length of the biologically active season (Block & Convey, 2001). This has been reflected in the growth rates of *C. aciphyllum* moss banks on Signy
Island which increased from a maximum of 2.4 mm y\(^{-1}\) in 1976 (Fenton, 1980) to 3.9 mm y\(^{-1}\) in 2009 despite windier and wetter summers reducing the instantaneous photosynthetic assimilation rate (Royles et al., 2012).

\section*{ii) Length of time the ground has been free from permanent snow and ice cover}

The AP and surrounding islands were ice covered during the LGM. Currently approximately 3.6\% (4300 km\(^2\)) of the land area of the AP, South Orkney and South Shetland Islands is ice-free (Peat et al., 2007), an essential requirement for the establishment of moss. The retreat of 87\% of AP glacier termini and reduced permanent snow cover (Cook et al., 2005, Strauss et al., 2009) provides land on which new moss banks could establish, and may re-expose moss tissue that can spontaneously regenerate new growth (LaFarge et al., 2013; Roads et al., 2014). Rapid glacier retreat on Ellesmere Island, Canada revealed viable bryophyte assemblages that had been buried under ice for up to 400 years (La Farge et al., 2013). Laboratory experiments show that Antarctic \textit{C. aciphyllum} has the capacity for regrowth from shoots at least 1500 years old (Roads et al., 2014). Although photosynthesis can occur through a limited snow covering, changes in snow cover patterns over time could explain periods of very slow / negligible peat accumulation that are evident in some age-depth models (e.g. Björck et al., 1991b, Royles et al., 2012), but the capacity for re-establishment of growth following subsequent alterations to snow distribution is also becoming clear.

\section*{iii) Stability of the substratum}

Moss banks require stable rock or soil in order to establish and accumulate (Fenton & Smith, 1982) so volcanic soils, areas undergoing substantial frost heave and beaches are unsuitable. Changes in the extent and depth of permafrost will impact the stability of the substratum more rapidly than substantial geological changes. On Signy Island, the active layer thickness is projected to increase at 10 mm yr\(^{-1}\) (Cannone et al., 2006). In 1976 the depth of seasonal \textit{C.}
aciphyllum bank thaw was 210±10 mm (Fenton, 1980), by 2009 the thaw in the same banks
was 300±10 mm (Royles et al., 2012). This 40% increase in seasonally unfrozen biomass was
coincident with an increase in mean annual temperature (MAT) of 0.9°C (Quayle et al.,
2002); however, there can be substantial inter-annual variation in permafrost depth
(Guglielmin et al., 2014). Further south, in Victoria Land, continental Antarctica the active
layer depth has increased at approx. 0.3 cm yr⁻¹ since 2000, which has altered soil stability
and decreased water availability to mosses (Guglielmin et al., 2014).

iv) Biotic disturbance

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

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

Antarctica is windy: on the South Shetland Islands the mean wind speed is 26 km hr⁻¹, with
gusts frequently over 100 km hr⁻¹ (Bañón et al., 2013). Furthermore, summer and autumn
wind speeds significantly increased (by 7-27% in summer) between 1980 and 2002 in the
latitude band from 50 to 65°S (Korhonen et al., 2010). With increased wind speed the rate of
erosion is likely to increase (especially with the increased depth of the active layer), and the
rate of evaporation will increase from the surface of soils and mosses. Although the mass of a
bank largely buffers the overall water content (Gimingham & Smith, 1971), if the surface
water film evaporates, the growing apices may become increasingly water limited and
desiccated.

vi) Nutrient status

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

vii) Water supply

The form and timing of precipitation are critical to the establishment, growth and
development of plants. Indeed, water supply is the most important physical driver of
Antarctic terrestrial communities and limits floral distribution across the continent (Convey et
al., 2014). Across the maritime Antarctic precipitation is frequent, with an increasing
proportion falling as rain rather than snow; however, water availability can vary very locally
which has a significant impact on the metabolic activity of plants (See sections 4&5)
(Schlensoeg et al., 2013, Wasley et al., 2012). The capacity for capillarity may limit the depth
to which poikilohydric moss tissue can accumulate as exposed growing tips lose water
through evaporation (Melick & Seppelt, 1997).

viii)  **Slope**

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

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

3. **Moss accumulation rates across Antarctica**

Fewer than 30 species of the known moss flora of Antarctica have been identified south of
67°S, and none are currently thought to be endemic to the very cold and dry continental
region (Ochyra *et al.*, 2008, Peat *et al.*, 2007). Whilst across the AP diversity decreases at
higher latitudes (Peat *et al.*, 2007), the continental distribution of plants suggests that it is
local microclimate conditions, particularly water availability, that are critical in determining
floral diversity (Cannone *et al.*, 2013, Colesie *et al.*, 2014, Convey *et al.*, 2014, Green *et al.,*
2011). Vegetation surveys across Antarctica have been very limited spatially and temporally,
with basic species presence and proportion cover records mainly focussed around research stations (Chown & Convey, 2007). It is rare for the depth of moss growth to be recorded; in situ experimental systems, to measure rates of moss growth, are difficult to establish and repeat visits to assess changes are rare. Consequently, there is limited baseline information available on Antarctic bryophytes from which any past or future effects of climate change can be assessed.

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

The uneven species’ distribution across Antarctica complicates the comparison between moss growth in the eastern and western regions, but the responses do provide contrasting markers for different life forms and climatic extremes. In the absence of detailed laboratory comparisons of physiology and growth under controlled environment conditions, we feel this broad comparison is informative. Whilst the moss peat accumulations in the maritime Antarctic region reach a maximum depth of 3 m on Elephant Island (Björck et al., 1991b), the continental Antarctic moss associations rarely reach 10 cm (Melick & Seppelt, 1997). Combining published age-depth profiles from moss accumulations from the Windmill Islands (Clarke et al., 2012), with those from Lazarev Bay (Convey et al., 2011, Royles et al.,
2013a) and Signy Island (Royles et al., 2012) since 1960 it is apparent that the rate of moss organic matter accumulation in the maritime Antarctic is at least three times higher than that in continental Antarctica (Figure 3).

Within the continental Antarctic mosses, the accumulation of C. purpureus in the Windmill Islands, which prefers drier habitats (Robinson et al., 2000), is slower than that of the more mesophytic B. pseudotriquetrum and Bryoerythrophyllum recurvirostre (Hedwig) from the Vestfold Hills (Clarke et al., 2012). Compression and decomposition are not taken into account, but as the measurements are made on individual shoots up to only 50 mm long, the effects of both processes are minimal. In the maritime Antarctic region, the similarity in accumulation rate between the Lazarev Bay and Signy Island banks since 1960 is interesting, as they lie at opposite extremes of the distribution range, approximately 1500 km apart, and are comprised of P. strictum and C. aciphyllum respectively. At both locations the top 100 mm of peat, within which zone compression will be minimal, has accumulated since 1988, at approximately 4 mm yr\(^{-1}\). Using bulk density measurements, the peat accumulation rate at Signy Island can be compared with that previously published at Lazarev Bay (Figure 4; Royles et al., 2013a). Whilst accumulation reached a peak at Lazarev Bay in the 1970s (briefly over 0.1 g DM cm\(^{-2}\) yr\(^{-1}\), when smoothed over three successive time-points), the rate at Signy Island reached a peak in the 1990s, at 0.06 g DM cm\(^{-2}\) yr\(^{-1}\). Both start to increase from around 1950 and the most recent measurements are similar at around 0.04 g DM cm\(^{-2}\) yr\(^{-1}\). Similarly in continental Antarctica, where moss growth rate was inversely proportional to summer wind-speed, and proportional to the number of days above 0\(^\circ\)C and to summer temperature, the Windmill Island mosses had maximum growth rates in the 1950s-1980s that subsequently fell in the 90s and 00s. However, at the Vestfold Hills the most recent moss growth rates have been highest (Clarke et al., 2012). The length of the growing season is a critical determinant of moss growth rate in both continental (Clarke et al., 2012) and AP
locations (Royles et al., 2012). The length of past growing seasons cannot be determined
directly from moss-cores, but estimates have been made by combining accumulation rates
derived from radiocarbon dating with stable isotope proxies for assimilation rate (Royles et
al., 2012).

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

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

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

$$\delta^{13}C = (R_{\text{SAMPLE}}/R_{\text{STANDARD}}) - 1$$
Source independent photosynthetic carbon isotope discrimination ($\Delta^{13}C$) can then be derived, if $\delta^{13}C$ values are known for both the plant ($\delta^{13}C_p$) material and the source CO$_2$, usually atmospheric CO$_2$ ($\delta^{13}C_a$):

$$\Delta^{13}C = \delta^{13}C_a - \delta^{13}C_p / (1 + \delta^{13}C_p)$$ (Farquhar et al., 1989).

$\Delta^{13}C$ is dominated by the biochemical fractionation of the carboxylase enzyme RuBisCO, having a value of around 29‰ in C$_3$ plants (O’Leary, 1988). This maximal fractionation is proportionally inhibited by resistance to CO$_2$ diffusion, leaving assimilates (and subsequently plant tissue) $^{13}C$-depleted compared to atmospheric, source CO$_2$ inputs. In astomatous bryophytes, the external water layer is a critical determinant of diffusion resistance and, consequently, the extent of discrimination against $^{13}CO_2$. Real-time measurements on liverworts, Sphagnum moss and Syntrichia ruralis show that a reduction in the external water layer is associated with an increase in instantaneous discrimination against $^{13}CO_2$ and in assimilation rate (Meyer et al., 2008, Rice & Giles, 1996, Royles et al., 2013b, Williams & Flanagan, 1996). As a proportion of the assimilated carbon is used to synthesise the structural carbohydrate cellulose, a major degradation-resistant component of bryophyte organic matter, the carbon isotope ratio of moss cellulose ($\delta^{13}C_C$) is a good proxy of the assimilation conditions during photosynthesis (Royles et al., 2012). Antarctic moss tissue $\delta^{13}C$ values are dependent on wind speed, temperature (both of which influence water availability) and ozone depth (which is linked to the phase of the Southern Annular Mode, and, consequently, wind-speed) (Clarke et al., 2012, Robinson & Erickson III, in press).

Measurements of the $^{13}C$ composition of Antarctic moss have been carried out on different species (including P. strictum, C. aciphyllum and C. purpureus), with different growth habits (large banks, hummocks and small cushions), with concurrent measurements back to the 1960s (Clarke et al., 2012, Royles et al., 2013a, Royles et al., 2012). Whilst $\delta^{13}C$ was
measured in whole organic matter for *C. purpureus*, most measurements on *C. aciphyllum*
and *P. strictum* were made on cellulose; however, comparative measurements of organic
matter and cellulose had a highly significant linear relationship (Royles, 2012) so $\delta^{13}C_{OM}$
measurements could be derived. Over the 60 y period under consideration in these
environments in which the rate of degradation is low, the compound specific diagenetic
effects that are an important factor to consider over long time periods should not be
substantial. There is a significant depletion in the composition of all the moss tissue over
time due to the assimilation of atmospheric CO$_2$ which is globally becoming more depleted
following the combustion of fossil fuels (Figure 5a) (Friedli *et al.*, 1986).

Source-independent $\Delta^{13}C$ was calculated for each measurement (Farquhar *et al.*, 1989),
dependent upon the isotopic composition of atmospheric CO$_2$ (Rubino *et al.*, 2013) at the
time of synthesis (as derived from $^{14}C$ measurements and estimated from age-depth model;
(Figure 5b)). Any contribution to assimilated carbon from sources of respiratory CO$_2$, such as
those associated with microbes or moss decay, were not included in the calculation of $\Delta^{13}C$.
Overall rates of respiration and microbial metabolism are low (Royles *et al.*, 2013a) and the
exposed banks are generally well-coupled to the atmosphere in the prevailing windy
conditions. Were any respiratory CO$_2$, with a source isotope composition close to that of bulk
material, to be refixed, it would tend to slightly increase the $\Delta^{13}C$ values to a similar extent at
all water contents. This response is not consistent with the declining $\Delta^{13}C$ seen in Signy
Island moss banks (Royles *et al.*, 2012), associated with warmer and wetter growth (and
presumably higher respiration rates) over the past decade.

Despite the species variation and geographic separation of up to 5000 km between sites, the
measured $\Delta^{13}C$ values are very similar, covering a 4‰ range from 17 to 21‰. The Lazarev
Bay moss had the highest source independent discrimination with the exception of 1970
when one *C. purpureus* value was higher. The lowest discrimination values of 17‰ were
measured on Signy Island, with the three *C. purpureus* and three *C. aciphyllum* cores largely overlapping in values between 17‰ and 20‰. When the Signy Island and Lazarev Bay ∆\(^{13}\)C\(_C\) values are considered back to 1850, the Lazarev Bay values show higher discrimination, which could be due to the species effect i.e. the Signy core is comprised of *C. aciphyllum*, whilst the Lazarev core is *P. strictum*, two species which have different anatomies and external water layers, along with potentially different metabolic responses to environmental conditions. In all the cores, the source independent discrimination was higher in 2000 than at the start of the record, with one of the Signy Island cores showing a 3‰ increase, with a 2‰ range at Lazarev and 1.5-2‰ elsewhere on Signy. On Signy Island the majority of the increase in ∆\(^{13}\)C occurred prior to 1960, compared with the substantial increase being measured from 1960 onwards at Lazarev Bay.

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

Without roots and with limited conduction systems, mosses are dependent on precipitation, dewfall or ground water for hydration and the isotopic composition of this source water (δ\(^{18}\)O\(_{SW}\)) is an important determinant of cellulose isotope composition (δ\(^{18}\)O\(_C\)). Globally, the composition of source water depends on various factors, the most relevant for
Antarctica being the form and amount of precipitation. Following initial evaporation from seawater (generating water vapour isotopically depleted in $^{18}$O) successive precipitation events (which favour the remaining heavy isotopes) become progressively depleted due to a Rayleigh distillation (Gat, 2000). Snow (and subsequent snow melt water) is more isotopically depleted than rain, and precipitation is also more depleted at high latitudes. However, even if the water source is known, $\delta^{18}$OSW is often unequal to the isotopic composition of leaf water ($\delta^{18}$OL) at the site of cellulose synthesis due to preferential evaporation of lighter water isotopologues ($\text{H}_2^{16}$O). Additionally, under high humidity conditions the rate of diffusive vapour exchange may be sufficient to imprint $\delta^{18}$OL with the atmospheric vapour isotope signal rather in place of $\delta^{18}$OSW (Helliker & Griffiths, 2007). Furthermore, there is an approximately 27‰ biochemical fractionation during the synthesis of organic matter, either following direct transfer of the $\delta^{18}$OL signal to sugars formed during photosynthesis and thence to organic material, or after re-equilibration of carbonyl groups that exchange with oxygen atoms in the surrounding water during the metabolic pathway of incorporation into storage polysaccharides (Barbour, 2007, Da Silveira et al., 1989, DeNiro & Epstein, 1979, Sternberg et al., 2006). The biochemical fractionation factor may be temperature dependent, with particular sensitivity at low temperatures (5-15°C) (Sternberg & Ellsworth, 2011) which would be highly relevant to Antarctic plants.

Thus, there are multiple factors that influence the measured oxygen isotope composition of bryophyte material at any particular time or place, with further complexity introduced from morphological and physiological differences between species. Factors which affect desiccation tolerance, the timing of cellulose synthesis relative to the extent of saturation, and microclimate and micro-topographical effects on relative humidity around the leaf could all affect the extent of evaporative enrichment. On Signy Island, there was a consistent offset in the oxygen isotope composition of cellulose between material obtained from low lying
hummocks, and more extensive moss banks (Royles et al., 2013c). This was attributed to the dominant water source in the former being more depleted snow melt water as compared to summer precipitation.

The extent of capillary water is an important determinant of both the carbon and oxygen isotope compositions, but $\delta^{18}O_C$ is less dependent upon the photosynthetic rate than $\delta^{13}C_C$ where, in combination with the capillary water, photosynthetic rate largely determines the diffusive supply of CO$_2$ from the atmosphere to the chloroplast (Rice & Giles, 1996, Royles et al., 2013b, Williams & Flanagan, 1996). The oxygen signal is largely dependent upon the difference in relative humidity between the moss tissue and atmosphere. The two isotope signals also represent subtly different time points. Whilst the $\delta^{13}C_C$ signal represents atmospheric CO$_2$ the external water layer thickness and internal conductance during carbon assimilation, $\delta^{18}O_C$ reflects the time of cellulose synthesis, when most oxygen atoms will exchange and re-equilibrate with contemporary tissue water. Experimental evidence from the desiccation tolerant moss $S. ruralis$ suggests that this temporal separation may be important, with $\delta^{13}C_C$ reflecting the time of maximum assimilation, just prior to metabolic limitation due to desiccation, whilst cellulose synthesis occurs following re-saturation with source water after rain / dewfall (Royles et al., 2013b) as turgor pressure is required for cell wall expansion and growth (S. A. Robinson pers. comm.). For moss banks and hummocks that experience lower daily fluctuations in water content than $Syntrichia ruralis$, the separation between periods of maximum assimilation and maximum cellulose synthesis are likely to be less distinct. Further experimentation under controlled environmental conditions is required to define these responses more generally.

With multiple factors influencing the measured $\delta^{13}C$ and $\delta^{18}O$ values, here we consider the values in tandem, in an attempt to identify biologically relevant clusters (Figure 7). Measurements of $\delta^{13}C_C$ and $\delta^{18}O_C$ have been made on $C. aciphyllum$ and $P. strictum$ from
extensive moss banks and hummocks on Signy Island, and from a hummock at Lazarev Bay on Alexander Island (Figure 7) (Royles et al., 2013a, Royles et al., 2012, Royles et al., 2013c). ∆\(^{13}\)C\(_{\text{C}}\) values were used to remove the impact of the systematic isotopic depletion in atmospheric CO\(_2\) over the industrialised period; however, a source effect was not removed from δ\(^{18}\)O\(_{\text{C}}\), as there was no independent record of source water composition. When both δ\(^{13}\)C and δ\(^{18}\)O measurements are considered the data points separate into three clusters:

1) *C. aciphyllum* from extensive Signy Island banks (∆\(^{13}\)C = 14-17‰, δ\(^{18}\)O = 26-31‰)

2) *C. aciphyllum* from small Signy Island hummocks (∆\(^{13}\)C = 15-17‰, δ\(^{18}\)O = 22-27‰)

3) *P. strictum* from Signy Island and Lazarev Bay (∆\(^{13}\)C 17-19.5‰, δ\(^{18}\)O = 23-27‰)

This can also be characterised as:

1) *C. aciphyllum*: ∆\(^{13}\)C< 17‰;

2) *P. strictum*: ∆\(^{13}\)C >17‰

2) Hummock (e.g. Fig. 2f): δ\(^{18}\)O < 26‰;

Bank (e.g. Fig. 2a): δ\(^{18}\)O >27‰

Several factors underlie these groupings. Species has a dominant effect on ∆\(^{13}\)C. Lamellae on the leaves of *P. strictum* facilitate relatively faster diffusion of CO\(_2\) into the leaf as compared to *C. aciphyllum* under the same moisture conditions, hence the higher discrimination. *Chorisodontium aciphyllum* is dominant in wetter areas whilst *P. strictum* is associated with drier conditions, (Fenton & Smith, 1982), as, being endohydric, *P. strictum* has some capacity for internal water transport which enables tissues to maintain hydration for longer in dry conditions. It is surprising not to see a latitude effect in *P. strictum* δ\(^{18}\)O values, as being 9° further south than Signy Island, the isotopic composition of precipitation at Lazarev Bay would be expected to be more depleted in \(^{18}\)O values. In contrast, whilst the carbon isotope composition of all the *C. aciphyllum* samples falls within the 14-17‰ range, the oxygen isotope composition of cellulose from bank-forming *C. aciphyllum* is significantly higher.
than that from hummock forming *C. aciphyllum*. This offset can be attributed to the inputs of isotopically lighter summer precipitation, as compared to more depleted melt water, and also influenced by the extent of evaporative enrichment (Royles *et al.*, 2013c).

Variation in δ¹³C and δ¹⁸O measurements of 3‰ and 4‰ respectively remains within the clusters, and indeed individual cores, representing variation measured over time that reflects local environmental changes. Photosynthetic conditions can vary locally, as cryo-perturbation makes the moss surface uneven at the centimetre scale, with the tops of ridges being driest and windiest (Lovelock & Robinson, 2002, Lucieer *et al.*, 2013). This can affect both Δ¹³C and δ¹⁸O measurements, with higher Δ¹³C values associated with drier conditions and higher δ¹⁸O with a greater degree of evaporative enrichment. On the millennial scale that the *C. aciphyllum* core data represents, differential rates of growth and the disturbing effects of winter snow cover may alter the relative positioning of the growing moss within the local micro-topography. Thus, the stable isotopic composition of mosses over time is dependent upon species and can provide information about the growth form and microclimate conditions at the leaf surface, as well as reflecting to some extent the narrow range of environmental conditions which support growth.

Not all isotopic variation can currently be attributed to a particular environmental factor, hence more laboratory work is required to elucidate under controlled conditions some of the drivers of the variation (such as the influence of temperature on isotope fractionation factors during cellulose biosynthesis (Sternberg & Ellsworth, 2011)) and also additional proxies could be analysed to provide more information about the past. For example, the analysis of δ²H, alongside ¹⁸O isotopomers, could be used to compare the δ²H–temperature relationship along modern elevation and latitude gradients. In this way, *Sphagnum* δ²H from a Patagonian peat bog was used to reconstruct the past meteoric water composition and
revealed abrupt temperature changes during the late Pleistocene and early and middle Holocene (Pendall et al., 2001). By combining $\delta^{2}H$ and $\delta^{18}O$ values from organic compounds it is possible to estimate the meteoric water composition at the time of synthesis, and potentially estimate temperature and relative humidity conditions that could result in the measured isotope values (Edwards, 1993, Edwards et al., 2000).

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

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

Photosynthetic light use can be estimated using chlorophyll fluorescence as a non-destructive measure of photosystem activity, allowing quantum yield ($\Psi_{PSII}$), electron transport rate (ETR) and energy dissipation (non-photochemical quenching, NPQ) to be determined for Antarctic mosses under laboratory (Stanton et al., 2014) and field conditions (Robinson et al., 2000, Schlensog et al., 2013) to show, for example, the relative sensitivity of mosses to desiccation (Robinson et al., 2000). The mesic mosses *Bryum argentum* and *B. pseudotriquetrum* had sufficient water for continuous metabolism with seasonally integrated
ETR (representing assimilation) largely dependent upon light and temperature (Schlensog et al., 2013). In contrast, the most xeric mosses (*C. purpureus*, *Stereocaulon alpinum* and *Andreaea gainii*) were only active for 40-50% of time. With 60% activation *Polytrichum alpinum* was the most active xeric moss as being endohydric it has as some capacity for water transport and a cuticle to reduce the rate of water loss (Schlensog et al., 2013).

By following photosynthetic gas exchange and isotope discrimination during a drying curve stable isotope physiology and hydrology can be investigated (Rice & Giles, 1996, Royles et al., 2013b, Williams & Flanagan, 1996). Chlorophyll fluorescence and derived characteristics (ETR, NPQ) can also be used to track photosynthetic activity and the impact of dehydration (Figure 8, J Royles, H Jenkins and H Griffiths, unpublished data). During desiccation, *S. ruralis* ETR increased as photosynthesis became less diffusion limited, reaching a maximum at a relative water content (RWC) of 150%; below 100% RWC, ETR declined rapidly as moss photosynthesis was compromised by desiccation (Figure 8a). This profile tracked the real-time carbon isotope discrimination signal (Royles et al., 2013b) and was consistent with ETR as an additional proxy for carbon uptake. Successive light response curves throughout the drying curve (Figure 8b) also show the overall responsiveness of fluorescence, and potential for the development of ETR as a remotely-sensed proxy for photosynthetic activity as a function of moss hydration status. Additional measurements on this system showed that the isotope composition of soluble carbohydrates can also be used to integrate daily carbon gain. The $^{13}$C signal ($\Delta^{13}$C=20±0.5‰ (n=8)) was indicative of optimal gas exchange, whilst the $^{18}$O signal was more sensitive to evaporative enrichment during desiccation (increasing from 21.7±0.8‰ to 25.1±0.6‰ (n=4 each)) as it was probably re-equilibrating with tissue water during growth in the light (J Royles, A Sturgess and H Griffiths, unpublished data). The rapid physiological responses of *S. ruralis* to RWC reflect
the tight coupling between the moss and current environmental conditions. We would expect
bank forming mosses, with less variable tissue water contents, to show somewhat buffered, or
muted, coupling between changing environmental conditions, fluorescence and isotope
signals. However, the prospects for resolving the variations within and between $^{13}$C and $^{18}$O
signals in Antarctic mosses seem promising (Figure 7), as well as the use of chlorophyll
fluorescence to investigate moss bank responses at ecosystem and regional scales.

6. Responses of polar mosses to climate change

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

i) Direct and indirect responses to temperature

For Antarctic bryophytes, chlorophyll fluorescence measurements were used to infer that the
extent of the hydrated (active) period was a more important influence on photosynthetic
performance than temperature, with reliance on melt water or more temporary activation
from precipitation being a key factor (Schlensog et al., 2013). Increases in temperature will
alter water availability to mosses through changes in the timing and extent of melt streams
and increases in active layer depth (Guglielmin et al., 2014). The speed with which plants
reactivate photosynthesis following both prolonged winter freezing, rapid freeze-thaw cycles
and periods of summer desiccation, is relevant to the seasonal assimilates preserved in
organic matter. Mesic Antarctic mosses take 24 h to fully recover net photosynthesis
following desiccation due to resaturation respiration (Schlensog et al., 2004), a transient
increase in respiration widely seen in anhydrobiotic organisms following rewetting, possibly
due to metabolic costs of repair, or mitochondrial inefficiency (Nijp et al., 2014).
Experimental warming was tentatively associated with a decrease in moss cover in the Arctic tundra, but the response varied substantially over space and time (Elmendorf et al., 2012) and with limited samples it is difficult to account for the influence of ambient conditions and species-specific dynamics (Lang et al., 2012, Street et al., 2013) especially as moss distribution may be more sensitive to moisture availability than warming (Lang et al., 2009).

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

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

Bryophyte photosynthetic activity is responsive to light intensity in moist habitats, but less so in more xeric habitats, where water limitation is the major determinant (Schlensog et al., 2013). Changes to cloud cover will alter light availability for photosynthesis, at Vernadsky station (Fig 1a) cloud cover increased significantly between 1960 and 2005 (Kirchgaßner, 2010). The growth of *Sphagnum* was directly related to light intensity in wetter sites in Alaska, where increasing water table and acidification were associated with a decline in black spruce (Fenton & Bergeron, 2006). In two recent extensive meta-analyses of peat accumulation, light availability was related to *Sphagnum* growth, particularly at high latitudes (Charman et al., 2013, Loisel et al., 2012). Indeed, total carbon accumulation in northern
peatlands over the past 1000 y was linearly related to photosynthetically active radiation
projected over the growing season (defined as the Growth Degree Days, for which air
temperature is greater than 0°C, GDD0), and with a stronger correlation than with GDD0
alone (Charman et al., 2013).

**iii) Responses to water availability**

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

An important additional consideration for the water relations of mosses is plant life-form and
functional type (filamentous, hummock/hollow (Turetsky et al., 2012)). There may be
separation between the photosynthetic tissues, which are usually restricted to the top 5 mm of
shoots and thus exposed to wind and hence dry out quickly, and water storage in spongy tissue below (Stanton et al., 2014). Rates at which individual shoots lose water to the atmosphere can be very different to that of whole clumps and capacity for internal water redistribution is a critical component of physiology. Similarly, the moss temperature can be much warmer than the air temperature (Longton, 1982, Smith, 1988b), and it is important to separate the effects of vapour pressure differences between tissue and atmosphere (VPD) and air temperature: VPD, which determines the rate of drying, varies non-linearly with temperature (Stanton et al., 2014). Indeed, polar mosses can have high rates of photosynthesis over a range of temperatures (Davey & Rothery, 1997, Pannewitz et al., 2005). The strong influence of VPD on moss photosynthesis in both C. purpureus and S. antarctici means that temperature, precipitation and VPD all need to be modelled accurately before conclusions can be drawn about the effects of climate change (Stanton et al., 2014).

7. Scaling physiological proxies to monitor and model climate change for the future

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

Firstly, one must distinguish between boreal forest (coniferous dominated, mainly north of 45°N) and tundra (8.2 M km², mostly north of 65°N) (Xu et al., 2013), and the contrasting responses of bryophytes and their associated carbon storage capacity (Charman et al., 2013, Sistla et al., 2013, Yu et al., 2010). Within this enormous range of habitats, three generalised
responses might be anticipated: (i) a northerly shift in vegetation boundaries associated with rapid warming and restricted extent of permafrost (Baltzer et al., 2014, Turetsky et al., 2012, Turetsky et al., 2010, Xu et al., 2013); (ii) increasing frequency and intensity of drought, and associated fires in more continental areas, likely to reduce Sphagnum dominance and increase conifers capable of regenerating after fire (Chapin III, 2003, Chapin III et al., 2010, Turetsky et al., 2012, Turetsky et al., 2010); (iii) increased precipitation in more maritime regions of Alaska and western Canada, as well as in Fennoscandia and Western Siberia, leading to enhanced Sphagnum growth, elevated water tables and forest decline associated with paludification (Crawford, 2008, Crawford et al., 2003, Fenton & Bergeron, 2006, Turetsky et al., 2012).

Key questions for the future relate to the development of methods and approaches needed to monitor these processes remotely, to allow modelling and predictions of climate change impacts to be validated (Chapin III et al., 2010, Crawford et al., 2003). In the Antarctic, we have recently seen the use of Landsat satellite images to project current vegetation distribution via Normalised Distribution Vegetation Index (NDVI: (Fretwell et al., 2011)) and spatial variations in moss bank surface temperature and spectral reflectance, estimated from an Unmanned Aerial Vehicle (UAV), mounted with sensors and cameras (Turner et al., 2014). Chlorophyll fluorescence has been used to ground-truth the responses of cryptogamic communities to water availability (Schlensog et al., 2013), and there is now the possibility of using the Laser Induced Fluorescence Technology (LIFT) as a remote-sensing system, across a range of spatial scales (Kolber et al., 2005, Pieruschka et al., 2012). Finally, the interpretation of solar-induced fluorescence from UAVs (Damm et al., 2014) or satellite systems (Zhang et al., 2014) has recently been provided with a quantitative framework to interpret components such as quantum yield, ETR and NPQ (Guanter et al., 2014). The opportunity for their use in distinguishing moss photosynthetic activity and carbon
sequestration as a function of water availability, across a changing forest mosaic, and at regional scales for polar regions, is now a realistic prospect. There will be exciting opportunities for ground-truthing these remote proxies under challenging Arctic and Antarctic conditions.

8. Conclusion

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

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**Figure Legends**

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

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) Rridged 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.

Figure 3: Age-depth models developed from bomb-spik e 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).
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.

Figure 5a): Measured δ\(^{13}\)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) δ\(^{13}\)C was measured in cellulose. Comparative measurements of organic matter and cellulose showed a highly significant linear relationship between δ\(^{13}\)C\(_{OM}\) and δ\(^{13}\)C\(_C\) (R\(^2\)=0.73, p<0.0001, n=40, F=108, y=0.75x – 4.58) from which δ\(^{13}\)C\(_{OM}\) were derived; b) Source-independent discrimination (Δ\(^{13}\)C) was calculated for each measurement (see text for details; NB. Different y-axis scales).

Figure 6a) Measured carbon isotope composition of cellulose (δ\(^{13}\)C\(_C\)) and b) Source independent discrimination (Δ\(^{13}\)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).

Figure 7: Extent of source independent carbon (Δ\(^{13}\)C) and oxygen (δ\(^{18}\)O) isotope discriminations measured in cellulose for Signy Island Chorisodontium 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). δ\(^{13}\)C and δ\(^{18}\)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.

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)
Figure 1a) Map of Antarctica and summer temperature trends
261x189mm (96 x 96 DPI)
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.
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 pseudotrigatum 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).
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 δ13C 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) δ13C was measured in cellulose. Comparative measurements of organic matter and cellulose showed a highly significant linear relationship between δ13COM and δ13CC (R2=0.73, p<0.0001, F=108, y=0.75x - 4.58) from which δ13COM were derived; b) Source-independent discrimination (∆13C) was calculated for each measurement (see text for details; NB. Different y-axis scales).
Figure 6a) Measured carbon isotope composition of cellulose ($\delta^{13}C_C$) and b) Source independent discrimination ($\Delta^{13}C$; 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).
Figure 7: Extent of source independent carbon ($\Delta^{13}C$) and oxygen ($\delta^{18}O$) isotope discriminations measured in cellulose for Signy Island Chorisodontium 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.
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).

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