Ecology of moss banks at Signy Island (maritime Antarctica)

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ABSTRACT

Mosses are dominant components of high latitude environments. Signy Island (maritime Antarctic) provides a representative example of polar cryptogam-dominated terrestrial ecosystems. In 2011 we mapped all moss banks, their characteristics (thickness, area, floristic composition) and investigated their relationship with selected environmental factors including topography (elevation, slope, aspect), biotic disturbance (fur seals), deglaciation age of the surfaces, location on the eastern vs. western side of the island, and snow cover (as a proxy of water supply during the summer - December).

We here identify the most important environmental factors influencing moss bank characteristics and distribution and provide a baseline for future monitoring. Moss bank abundance and distribution are the result of the interaction of multiple abiotic and biotic factors acting at different spatial scales. The most important factors are the location of moss banks on the eastern vs. western side of the island at the macroscale (with thicker and larger moss banks and a prevalence of *Chorisodontium aciphyllum* on the western side), and their favorable aspect (mainly N, NW) at the microscale, providing better microclimatic conditions suitable for their development. The elevation threshold detected at 120 m could indicate the occurrence of a “moss bank line”, analogous to the treeline, and corresponds with a threshold of mean annual temperature of -4.8°C. The other factors examined play a subsidiary role in affecting bank distribution and characteristics. These findings allow a better understanding of this key feature of maritime Antarctic vegetation and provide quantitative information about their ecology.

KEYWORDS: Mosses; Environmental factors; Antarctica; Topography; Biotic and abiotic disturbance; Fur seal; Deglaciation age; Westerly winds.

INTRODUCTION

Mosses are ubiquitous components of plant communities in high latitude ecosystems, becoming dominant in terms of diversity and biomass in the High Arctic (Meltofte, 2013) and, particularly, in the Antarctic, where vegetation is dominated by cryptogams (Longton, 1988; Ochyra *et al.*, 2008; Convey, 2013; Cannone *et al.*, 2013). The importance of mosses is well demonstrated in key ecosystem processes relating to nutrient, carbon and water cycling, permafrost formation and thaw, and peat (carbon) accumulation. Many moss species occupy restricted ecological niches and are sensitive to ecological and climatic change (Van der Putten *et al.*, 2009), as demonstrated by the abrupt changes detected in moss communities in response to past climate changes (e.g. Jonsgard & Birks, 1995; Van der Putten *et al.*, 2009, 2012), indicating their potential sensitivity to contemporary and future climate changes, especially at high latitudes.

Moss peat banks are a characteristic and unique feature of Antarctic vegetation because they differ from most peat deposits, which usually develop on poorly-drained ground or in wet depressions associated with water saturation and anaerobiosis. Antarctic moss peat banks (moss banks) are characterised by low humification and a lack of water saturation, and receive moisture supply mainly from precipitation (semi-ombrotrophic) (Fenton & Smith, 1982; Royles *et al.*, 2012). These banks develop due to the erect growth form of the component species (being in most cases the tall turf-forming mosses *Polytrichum strictum* Brid. and/or *Chorisodontium aciphyllum* (Hook.f. & Wilson) Broth) (Gimingham & Smith, 1971), combined with the low temperature and pH (3.5-4 5) of the peat (inhibiting microbial activity) and the occurrence of permafrost (Fenton & Smith, 1982; Roads *et al*., 2014). Banks can accumulate considerable thickness (up to 3 m) (Allison & Smith, 1973; Smith 1981), age ≥ 6000 years (Björck *et al.*, 1991), with growth rates ranging between 0.6 mm/y to more than

5 mm/y depending on their specific location and age (e.g., Royles *et al*., 2012, 2013). These features develop only under favorable climatic conditions characterized by cool and wet summers and, recently, Royles *et al*. (2012) emphasized their sensitivity to recent climate change, demonstrated by a progressive increase of their growth rate detected at Signy Island from 0.6 mm/y before the industrial revolution, to 2.3 mm/y (period 1950-2010), and 3.9 mm/y (period 1980-2010) in response to increased growing season length, and warmer and wetter summers.

Moss banks have a disjunct distribution ranging from c. 51°S in the Falkland Islands to c. 69°S in the Antarctic Peninsula, showing the largest abundance and being widespread in maritime Antarctica, particularly in the South Orkney Islands (e.g., Fenton & Smith, 1982; Van der Putten *et al*., 2009, 2012; Convey *et al*., 2011; Royles *et al*., 2012, 2013). Within this archipelago, Signy Island has been recognized to be a representative example of polar cryptogam-dominated ecosystems, illustrating the structure and dynamics of Antarctic terrestrial ecosystems in general (Smith, 1990). In the 1970s Fenton & Smith (1982) mapped in detail the spatial distribution of these features on Signy Island and hypothesized that the main abiotic and biotic factors influencing them were (i) length of the time the ground is snow free in summer; (ii) length of time the area has been free from permanent snow in the past; (iii) biotic disturbance; (iv) harshness of the environment (with specific reference to wind as a critical factor related to altitude); (v) water supply; and (vi) slope. However, these relationships were analyzed and described largely in a qualitative manner and based on examination of a restricted sub-set of the moss banks mapped. Furthermore, in their analysis Fenton & Smith (1982) did not consider that Signy Island is characterized by the occurrence of strong westerly winds (Zazulie *et al.*, 2010). Elsewhere, the limiting action of wind can result in asymmetric patterns in vegetation distribution, as noted in the sub-Antarctic (e.g., Macquarie Island, see Adamson *et al.*, 1993; Selkirk & Saffigna, 1999; Marion Island, see Haussmann *et al.*, 2009). Moreover, at Signy Island the potential effect of westerly winds on vegetation could be enhanced by the topography of the island, specifically by the island having a N-S oriented relief, which could result in greater precipitation on the windward (western) side of the island and thereby induce an asymmetry in vegetation patterns. Such a phenomenon has been documented for many N-S oriented mountain systems in coastal regions globally (e.g., California, Chile and New Zealand) (e.g., Lundquist *et al*., 2010; Lenaerts *et al*., 2014; Sturman & Wanner, 2001).

The uniqueness of moss banks and their potential sensitivity to future climate changes highlight the need to investigate their ecological requirements and distribution patterns. Therefore, we performed a detailed mapping of the moss (peat) banks occurring at Signy Island, recording their characteristics and relationships with the main abiotic and biotic environmental factors. We hypothesized that: 1) the impact of favourable aspect (north-facing) (at the scale of individual moss banks - microscale), and location on the eastern vs. western side of the island (at the scale of the entire island - macroscale) would be the most important environmental factors influencing moss bank characteristics; 2) the deglaciation age of the underlying surfaces would influence the abundance and thickness of moss banks; and 3) the interaction with long-lasting snow cover in summer may influence their floristic composition. The survey results also provide a robust baseline for future monitoring, allowing qualitative and quantitative assessments of future climate and environmental change impacts.

STUDY AREA

Signy Island (60°43'S, 45°38'W; South Orkney Islands, maritime Antarctic) is characterised by a cold oceanic climate, with mean annual air temperature of −3.5 °C and annual precipitation ranging from 350 to 700 mm, primarily as summer rain (Smith, 1990; Jones *et al.*, 2000; Royles *et al.*, 2012). It is also characterised by prevailing westerly winds linked to the Southern Annular Mode (SAM, Zazulie *et al.*, 2010), which have exhibited changes consistent with anthropogenic forcing since the 1970s, as well as a 250 y periodicity over the last 2600 y in the Southern Hemisphere (e.g. Thomas *et al.*, 2015; Turney *et al.*, 2016a, b). Over the last 50 y Signy Island has experienced an increase of both air temperature and total annual precipitation (Turner *et al.*, 2009; Royles *et al.*, 2012; Cannone *et al.*, 2016). Signy Island also possesses a rapidly shrinking ice cap (losing >1 m/year in thickness over the last 20 y) (Favero-Longo *et al.*, 2012). Permafrost is continuous, with an active layer thickness ranging between 40 cm and more than 3 m (Guglielmin *et al.*, 2008a, 2012), that has recently been deepening by *c.* 1 cm/year in response to increasing air temperature (Cannone *et al.*, 2006).

The island's terrestrial habitats and its vegetation are well characterised, and are widely regarded as representative of the entire maritime Antarctic region, as well as of cryptogam-dominated fellfield habitats across the polar regions (Smith, 1972, 1984, 1990; Longton, 1988). Following the cessation of sealing on South Georgia and the recovery of the historically devastated fur seal (*Arctocephalus gazella* Peters 1875) population, in the latter half of the 20th Century resting and moulting fur seals started to be seen in the South Orkney Islands, with the first sighting at Signy Island in 1948 and the start of an annual fur seal census in 1977 (Waluda *et al.*, 2010). Since the late 1970s, Signy Island has experienced a very rapid increase in the numbers of resting and moulting predominantly male fur seals, accounting for c. 11200 ± 4100 individuals in 2008 (Waluda *et al.*, 2010). Fur seal activity can negatively impact vegetation, producing considerable damage by trampling/crushing (Smith, 1988), as well as though nitrogen release in faeces/urine (Favero-Longo *et al.*, 2011). It has also been recently documented that this recent rapid increase in fur seal numbers has affected the spatial distribution of *Deschampsia antarctica* and *Colobanthus quitensis* on Signy Island, the two only native vascular plants occurring in the maritime Antarctic (Cannone *et al.*, 2016).

METHODS

During January-March 2011, we carried out a field survey to map the abundance and spatial distribution of moss banks, identified by the occurrence of the tall turf-forming mosses *Polytrichum strictum* Brid. and *Chorisodontium aciphyllum* (Hook.f. & Wilson) Broth), both as single species stands as well as growing together (mixed stands), with a minimum thickness of 50 mm (Fenton & Smith, 1982). The data obtained in this survey are fully comparable with those of the survey performed in the 1980s (Fenton & Smith, 1982), but here we concentrate on our new survey data in order to identify influences on the ecology and distribution patterns of contemporary moss banks; changes in moss bank distribution and properties over time will form the subject of a separate publication.

Each moss bank was mapped and digitized using the best Digital Elevation Model (DEM) available for the island (resolution of 7.5 m) using ArcMap 10.1 and, considering the centroid of each moss bank, we computed its elevation (m a.s.l.), slope (°) and aspect (divided into eight sectors: N; NE; E; SE; S; SW; W; NW). The location of moss banks on the eastern or western side of the island was identified following the watershed divide/crest. We also recorded the following original data (not recorded in any previous survey) for each moss bank: a) dominant bank forming species (*C. aciphyllum* and/or *P. strictum*), b) maximum moss bank thickness, c) occurrence of vascular plant colonization, and d) presence/absence of fur seal disturbance, assessed on the basis of the visible health and indication of seal trampling/crushing and associated nitrogen release in faeces/urine. Moss bank thickness (mm) was measured for 262 of the moss banks (85%) probing in at least three different points of the bank and recording the maximum depth value, and using only these data for further analyses. For the remaining 48 moss banks (15%) only one measurement of thickness was performed in order to confirm that the bank exceeded 50 mm depth.

In polar environments and especially in Antarctica the importance of snow cover for water supply from snow melting has been widely recognized (e.g., Kennedy, 1995; Schlensog *et al*., 2013; Convey *et al*., 2014). To assess whether moss bank distribution is linked to long-lasting snow cover, we analyzed an infrared image taken over the entire island in summer (December 2010). Using this image we performed an unsupervised classification analysis using ArcMap 10.1 multivariate tools, in order to identify the areas covered by long-lasting snow. We then investigated the relationship between long-lasting snow and moss bank distribution by considering three classes: 1) no interaction, 2) direct interaction between moss banks and snow cover with direct water supply from snow melting, (3) indirect interaction as the moss bank was separated by $\geq$ 10 m from the snow boundary, with the potential for indirect water supply from snow melting.

In order to analyze the distribution of the moss banks with respect to the deglaciation age of the underlying surface we upgraded the reconstruction of deglaciation proposed by Smith (1990) by integrating all suitable published ^{14}C data available for Signy island (Fenton & Smith, 1982; Jones *et al*., 2000; Royles *et al*., 2012) and the geomorphological map of the island, as moraine ridges represent the limit of the maximum glacial advance after 6600 cal yr BP (Guglielmin *et al*., 2008b). We also included a new and previously unpublished AMS ^{14}C age of a re-exposed moss bank. All the ^{14}C data were re-calibrated using the software OxCal 4.2 (Bronk Ramsey, 2009) and the SHCal13 ^{14}C Southern Hemisphere atmosphere dataset (Hogg *et al*., 2013). The identified geomorphological phases of glacial evolution of the island were digitized in the same GIS system as the moss banks.

Data analyses

The main characteristics (area, thickness, floristic composition) and distribution patterns of moss banks were analyzed across the entire island with respect to abiotic (elevation, slope, aspect, long-lasting snow cover in summer, location on the eastern vs. western side of the island and deglaciation age) and biotic (fur seal disturbance) factors. For these analyses we used a non-parametric statistical approach based on the maximum and minimum values, median, 25% and 75% quartiles, providing a description of the core of the moss distribution (Maggini *et al*., 2011). Analyses were performed using the software Statistica®.

A multivariate analysis (Redundancy Analysis, RDA) was performed to analyze the relationships between moss bank characteristics (thickness, floristic composition, occurrence of *D. antarctica*) and topography (elevation, slope, aspect), snow cover, deglaciation age, location on the eastern vs. western side of the island and biotic disturbance. The RDA (log transformation of species data, performing the Monte Carlo permutation test on the first and all ordination axes) was performed using CANOCO 4.5 (Ter Braak & Šmilauer, 1998). We quantified the categorical variables as follows (Lepš & Smilauer 2003) Aspect: 1 = northern (N, NW, NE); 0 = east or west (E, W); -1 = southern (S, SW, SE); location on the eastern/western side of the island: 1 = E; W = 0; deglaciation age periods 3 = age > 6600 y cal BP; 2 = age 6600 – Little Ice Age (LIA); 1 = age post LIA; snow cover 1 = direct interaction; 0 = indirect interaction; -1 = no interaction; fur seal disturbance 1 = presence, 0 = absence. In the visualization of the RDA the area of moss banks was located very close to the origin, meaning that this parameter did not exhibit a clear pattern with respect to any of the selected environmental factors, and we thus do not report this here.

In addition to the RDA, the relationships of moss banks with biotic and abiotic factors were analysed using generalized linear/nonlinear models (GLZ), with the selection of the model with the best fit based on Akaike's information criterion (AIC). To identify the factors influencing the most important moss bank characteristics we performed two GLZ, selecting as dependent variable (a) moss bank thickness, (b) moss bank area. The GLZ were performed using the software Statistica®.

RESULTS

Main characteristics of banks and distribution patterns with abiotic and biotic factors

Prior to analyzing the moss bank distribution patterns in relation with the main abiotic factors, we considered the occurrence of fur seal disturbance. The impacts of this on moss banks were clearly associated with elevation, with the greatest impact close to sea level, and impact almost negligible above the elevation of 60 m a.s.l., which acted as a threshold (Table 1).

A total of 310 moss banks was recorded across the entire island (Fig. 1), occurring at elevations from sea level up to 202 m a.s.l., exhibiting a unimodal distribution (characterized by one peak of greatest abundance at intermediate values) with elevation (Fig. 2A) with a peak in occurrence between 21 and 60 m a.s.l. Median elevation was 52 m a.s.l., and 75% of the banks occurred below 80 m a.s.l. A unimodal distribution pattern was also evident with slope (Fig. 2B), with a peak between 10° and 21°, the median at 10°, and 75% of banks found on slopes ≤ 24°. In terms of aspect (Fig. 2C), more than 50% of the banks were present in N and NW facing areas, a proportion that increased to >70% when W facing banks were included.

Maximum bank thickness exhibited a median of 200 mm and a 75th quartile of 400 mm (Table 1) and was characterized by an exponential distribution ($p < 0.01$). No relationship was apparent between moss bank thickness and elevation ($p > 0.05$). The area of moss banks exhibited a median of 573.9 m^2 and a 75th quartile of 1412 m^2 (Table 1) and was again characterized by a unimodal distribution. The relationship between area and maximum depth (as tested by polynomial regression), despite being statistically significant ($p < 0.01$), had very low explained variance ($R = 0.16$), while the relationship between moss bank area and elevation was not statistically significant ($p = 0.5$).

Half of the moss banks were single species stands (32% composed only of *C. aciphyllum* and 18% of *P. strictum*), while 50% included both species. Both single species and mixed stands were found over the entire island (Fig. 3). A monospecific *C. aciphyllum* bank provided the highest elevation record (202 m a.s.l.), followed by mixed stands (189 m a.s.l.), while the maximum elevation of pure stands of *P. strictum* was lower, at 107 m a.s.l. (Fig. 4A). Both *C. aciphyllum* and *P. strictum* banks exhibited unimodal distribution patterns with elevation (Fig. 4A), with a peak at 41-60 m a.s.l. for the former, and 21-40 a.s.l. m for the latter. Conversely, the mixed stands were characterized by a bimodal pattern (characterized by two peaks of greatest abundance at intermediate values) with a main peak at 21-40 m a.s.l. and secondary peak at 81-100 m a.s.l. (Fig. 4A). Despite their different patterns, the distribution with elevation among the single species and the mixed stands did not show any statistically significant difference (t-test, $p > 0.05$). All bank types exhibited a unimodal distribution with respect to slope (Fig. 4B), with no statistically significant differences relating to their floristic composition ($p > 0.05$). Finally, there was a similar partitioning across the bank types among the eight aspect sectors, with a prevalence of records in the NW, N and W sectors (Fig. 4C), and a lack of statistically significant differences between patterns ($p > 0.05$). Only about 10% of the banks were colonized by the grass *D. antarctica*, these being mainly below 60 m a.s.l. (Table 1). Banks dominated by *P. strictum* showed the least evidence of disturbance by fur seals (26.7% of banks), while the levels of disturbance were greater and similar in those dominated by *C. aciphyllum* (52%) and the mixed stands (44.8%).

The extent of the area occupied by long-lasting snow cover during the summer accounted for 26.6% of the total ice-free area of the island. Almost a quarter (24.5%) of moss banks received direct water from snow melting, while 9.7% received only a potential indirect water supply, and 65.8% of moss banks did not receive water supply from snow melting at that time of season; these patterns were also evident at different elevations (e.g., below and above the elevation threshold of 60 m) (Table 1). The quantitative relation with snow cover differed between species: *C. aciphyllum* showed the highest proportion of banks having direct interaction with snow cover (37.7%, vs 22.4% of the mixed banks and 7.1% of *P. strictum*). In contrast, *P. strictum* showed the highest proportion of banks with no direct interaction with snow cover (84% vs 69.3% for the mixed stands and 51.1% for *C. aciphyllum*), while for all species the potential for indirect interaction was limited (12.2% for *C. aciphyllum*, 8.9% for *P. strictum* and 8.3% for the mixed banks).

At the macroscale, the comparison of the eastern vs. the western sides of Signy Island revealed that the numbers of moss banks were comparable across the two sides of the island (Table 2), with unimodal distribution patterns in relation to both elevation and slope, showing a peak between 21 and 60 m a.s.l. for the former and between 11° and 20° for the latter. Differences between the two sides of the island concerned the distribution of moss banks with aspect, as well as their maximum thickness (higher on the western side), area (larger on the western side) and floristic composition (with a prevalence of *C. aciphyllum* on the western side and of *P. strictum* on the eastern) (Table 2). The relationship of moss banks with snow cover was also asymmetrical, with a larger prevalence of no snow interaction on the eastern than on the western side (76.5% vs. 53.3%) (Table 2). This difference did not depend on the availability of long lasting snow cover in summer, which was similar across the two sides of the island (24.5% of available area on the eastern side and 28.1% on the western side of the island).

Deglaciation age of the underlying surfaces and distribution patterns of moss banks

To aid reconstruction of deglaciation during the Holocene, the oldest deglaciation age (before 6600 cal yr BP) was identified using the age of the basal ^{14}C of the cores of lacustrine sediments collected at Heywood and Sombre lakes (Jones *et al.*, 2000), while the limit of the maximum glacier expansion following 6600 cal yr BP was identified through the geomorphological map, considering the most distant moraine ridges from current ice fronts present in the different valleys and integrating this with the age of one re-exposed moss (n. 3 in Fig. 1; 617 cal yr BP). This last maximum glacier advance could be coincident with the Little Ice Age (LIA), consistent with the recent interpretation at Rothera Station (Adelaide Island, 68°S) of Guglielmin *et al*. (2016), where evidence from re-exposed mosses suggests that advance commenced between 671 and 558 cal yr BP and continued at least until 490–

317 cal yr BP. Therefore, three main periods of deglaciation age were identified at Signy Island (see Methods): I) surfaces deglaciated before 6600 cal yr BP (> 6600 yr BP, or oldest surfaces); II) surfaces deglaciated between 6600 cal yr BP and the Little Ice Age (LIA) (6600 – LIA, or older surfaces); III) surfaces deglaciated after the end of LIA (post LIA or youngest surfaces). In terms of topographic characteristics, measures of slope and aspect were comparable between these age classes, while the availability of different elevations changed substantially from the oldest and older surfaces to the youngest, with the latter being characterized by a larger availability of sites located above the elevation threshold of 60 m (Table 3).

The distribution of moss banks appeared to be directly related to the deglaciation age of the surfaces (Fig. 1) as both their abundance and thickness (but not their area) increased from the youngest to the oldest surfaces (Figs. 1, 5; Table 4). This trend did not depend on the surface available for moss colonization (largest for the oldest, but similar between the older and the youngest classes) (Table 3, Fig. 5). The proportion of moss banks on the eastern side of the island increased with decreasing age of deglaciation, reaching 100% for moss banks on the youngest surfaces (Table 4). The colonization of moss banks by *D. antarctica* also exhibited a pattern with deglaciation, increasing from the youngest to the oldest surfaces (Table 4).

Multivariate Analysis and Generalized Linear/non-linear Models

The redundancy analysis (RDA) (Fig. 6) explained 90.1% of the cumulative variance of the species-environment relationship (eigenvalues axes 1 and 2, respectively: X1 = 0.058; X2 = 0.047) and showed that the most important environmental gradients influencing the distribution of moss banks were their location on the eastern or western side of the island (F = 13.00, p = 0.005), and their northern facing aspect (in particular N, NW, NE) (F = 11.00, p =

0.005). Secondary factors were slope (F = 4.62, p = 0.005), elevation (F = 3.67, p = 0.01) and the interaction with long-lasting snow cover in summer (F = 2.37, p = 0.04). According to this clustering, most of the moss banks occurring on the eastern side of the island were characterized by N and NW aspect, a low level of interaction with long-lasting snow cover, larger abundance of *P. strictum* for the single species stands, lower influence of fur seals and colonization by *D. antarctica*, while the opposite conditions prevailed on the western side of the island.

The results of the RDA were corroborated by those of the two generalized linear/non-linear model (GLZ) analyses. The first GLZ, for which moss bank thickness was selected as dependent variable, showed that the most important factor was the location on the eastern vs. western side of the island, with thinner moss banks on the former, confirming the analyses presented in Table 2 and Fig. 6. The GLZ focusing on moss bank area as dependent variable showed that the most important factors were fur seal disturbance (but with an inverse relation, as the sites subject to fur seal disturbance had larger areas than the undisturbed ones) and snow cover (with larger area for moss banks with direct snow cover interaction).

DISCUSSION

Data and analyses in this study indicate that two main factors, acting at different spatial scales, are responsible for the distribution patterns of moss banks at Signy Island: their location on the eastern vs. western side of the island at the macroscale, combined with their northern facing aspect at the microscale. The first of these factors is taken into consideration here for the first time as an important driver of moss bank distribution, while the second has not been considered as playing an important role in previous studies. Our analyses identified other important factors including the interaction of moss banks with summer snow cover (as proxy for water supply) and fur seal disturbance, confirming the influence of water supply and biotic disturbance as proposed by Fenton & Smith (1982). Our data also document for the first time the separate contributions of the two moss bank forming species (*C. aciphyllum* and *P. strictum*) in shaping the distribution of banks across the island.

Role of topography and fur seal disturbance

The unimodal distribution patterns shown by moss banks in this study with respect to elevation and slope (Figure 2A, B) are similar to other analyses of the distribution of species richness with elevation in mountain areas (e.g., Rahbek, 1997; Grytnes & Vetaas, 2002). This type of pattern has been interpreted as the result of a combination of different factors including hard boundaries (i.e., the existence of ecophysiological limits and/or some degree of resistance to dispersal; Colwell & Lees, 2000), monotonic trends in species richness, and incomplete sampling (Grytnes & Vetaas, 2002). Given the thorough sampling achieved in the current study, the patterns obtained here are unlikely to be sampling artefacts. This implies that moss bank distribution is controlled by specific limiting factors at the distribution range boundaries (upper and lower), both for elevation and slope.

At the lower elevation boundaries of moss bank occurrence there was a very clear impact of fur seal disturbance. Our data indicate that the highest impact of fur seal disturbance occurs between 0 and 20 m a.s.l., and levels remain intense up to 60 m (Table 1), confirming the importance of biotic disturbance as an effective environmental factor involved in determining the extent of moss banks, as proposed by Fenton & Smith (1982). It has recently been demonstrated that the distribution patterns of the higher plants *D. antarctica* and *C. quitensis* on Signy Island are also influenced by fur seal disturbance, although in this case the impact is most strongly apparent only up to 20 m a.s.l. (Cannone *et al.*, 2016), with only limited damage apparent above that altitude. Mosses are clearly more vulnerable to this form of biotic disturbance than both higher plants and epilithic lichens (Smith, 1988; Favero-Longo *et al.*, 2011). However, it is also notable that, where fur seal disturbance was recognized, moss banks had larger areas and were thicker than in undisturbed sites, apparently in contrast with the existing literature (e.g. Smith, 1988; Favero-Longo *et al.*, 2011). Moss banks with fur seal disturbance occur at lower elevations than undisturbed ones (median values of 38 vs. 68 m a.s.l., respectively), and plausibly in sites characterized by more favorable environmental conditions both for moss growth (implying larger and thicker moss banks, likely existing before the onset of disturbance and potentially with higher resilience to damage) as well as for fur seal abundance. Our data also allow confirmation of the greater sensitivity of *C. aciphyllum* than *P. strictum* to fur seal disturbance (Fenton & Smith, 1982).

At the upper boundary of moss bank distribution, species ranges could be limited by physiological tolerances (which define their fundamental niche), as well as by biotic interactions and dispersal barriers (which further constrain the fundamental niche to the realized niche) (Tingley *et al.*, 2014). Although the maximum elevation recorded for an individual moss bank was 202 m (Fig. 2A, 4A), overall bank distribution patterns with elevation showed a clear altitudinal threshold, with a sharp decrease in numbers above 120 m. Despite the large availability of ice-free surfaces above 120 m, we hypothesize that the paucity of moss banks above this threshold could depend on disturbance factors limiting their initiation and subsequent development. One such driver could be air temperature, with lapse rates being almost linear with elevation (1.1°C/100 m on Signy Island, data not shown). The relatively small difference in elevation between upper and lower distribution boundaries (202 m), corresponds to ~ 2.2°C temperature difference, which could explain the observed patterns acting as a sort of "moss bank line" (similar to the treeline). Further confirmation of this hypothesis could be obtained by analysing the distribution of moss banks across Antarctica: the southernmost known location of of moss banks is at 69°S in Lazarev Bay (Convey *et al*., 2011) on Alexander Island, where they are located close to sea level. No data for mean annual air temperature (MAAT) for Lazarev Bay are available, and the closest location with available climatic data is San Martin station (68.1°S, 67.1°W, 4 m a.s.l.) with a MAAT of -4.8°C (period 1978-2015, source SCAR MET-READER). We therefore suggest that this is a potential temperature threshold controlling the formation of moss banks in Antarctica. At Signy Island the MAAT is -3.5°C, consistent with the temperature gradient provided by elevation at Signy Island explaining the lack of moss bank development at higher elevations. Indeed, the moss bank elevation threshold located at 120 m, given the local temperature lapse rate, would also represent an MAAT of c. -4.8°C.

Another factor which could contribute to defining the upper boundary of moss banks with elevation is wind exposure, which was proposed by Fenton & Smith (1982) as a limiting factor for moss bank distribution (describing its action as "environmental harshness"). Wind speed typically increases with elevation, and therefore also its erosive impact. Erosion could be effective both in damaging existing banks and in limiting the initial establishment of new moss growth, which is more vulnerable in the early years after establishment (Collins, 1976). Exposure to higher wind speeds may also keep bank surfaces clear of snow and hence directly exposed to both abrasion and winter temperatures well below zero (Collins, 1976). On sub-Antarctic Macquarie Island, wind disturbance has been recognized as the main environmental determinant of vegetation cover, showing an elevation threshold at 200 m a.s.l. (Adamson *et al.*, 1993). At Signy Island the mean annual wind speed at 80 m a.s.l. ranges between 3.6 and 4.5 m s^{-1}, with the daily maximum speed not exceeding 20 m s^{-1} (Guglielmin *et al.*, 2012). Nevertheless, at Jane Col (150 m a.s.l.) the mean annual wind speed is considerably higher, ranging between 5.5 and 6.7 m s^{-1}, with daily maxima exceeding 24 m s^{-1} on several days each year (unpublished BAS data). Based on these data, we suggest that it is reasonable to hypothesize that increasing wind speed between 80 and 150 m a.s.l. could be among the limiting factors contributing to the apparent threshold of 120 m a.s.l. at which there is a sharp decrease in moss bank development.

Our data clearly indicate the preference of moss banks for gentle slopes (with 75% located on slopes ≤ 24°), even though areas with more gentle slopes are often more accessible to fur seals. Multivariate analysis also emphasized that slope influenced moss bank distribution, with thinner moss banks being located on steeper slopes (Fig. 6).

Fenton & Smith (1982) stated that "aspect is not necessarily a limiting factor" influencing moss bank distribution. Our results contradict this hypothesis, detecting a clear bias towards northern and western slopes, with around 50% of moss banks located on N and NW slopes, increasing to 70% when the W slopes were included. The preferential location of moss banks in these aspect sectors implies microclimatic conditions more favorable to moss bank development. The role of aspect in providing favorable thermal conditions at the microscale is also corroborated by comparison of the ground surface temperatures (GST) of two areas of barren ground located at the same site (CALM grid) on Signy Island, with the same elevation and slope but with opposite aspect (N vs. S). Guglielmin *et al.* (2012) documented significant differences in both GST and thawing degree days (TDD), with the N facing area being warmer than the S facing, especially during the summer (≥30% for GST and ≥40% for TDD).

Role of snow cover

The form of the relationship between moss banks and long-lasting snow cover on the island at peak season could be considered a proxy of direct water supply. Our data indicate that only c. 25% of moss banks receive direct water supply from snow melting during the summer, consistent with their semi-ombrotrophic nature (Fenton & Smith, 1982; Royles *et al.*, 2012). Moreover, the pattern of moss bank interaction with snow did not depend on elevation (Table 1). Therefore, we suggest that snow cover does not act as a limiting factor for moss bank distribution, at least within their existing range of elevation, but that its influence affects primarily their floristic composition. The different ecological requirements of the two moss bank forming species likely underlies the observed differences in their quantitative relations with long-lasting snow cover. In particular, the larger proportion of moss banks dominated by *P. strictum* with no interaction with snow cover may relate to the fact that *P. strictum* is an endohydric species, showing some capacity for internal water transport which enables tissues to maintain hydration for longer in dry conditions, and possesses a cuticle that reduces the rate of water loss (Schlensog *et al.*, 2013; Royles & Griffiths, 2015).

Role of location on the eastern vs. western side of the island

Our data emphasize for the first time the role of this factor in shaping the distribution of moss banks on Signy Island. Despite overall similarity in bank abundance and distribution patterns with topography on both sides of the island, there were significant differences in terms of their thickness, area, floristic composition and interaction with snow cover (Table 2). The patterns of abundance of the more xeric species *P. strictum* and the more hygric species *C. aciphyllum* across the two sides of the island (Table 2) support the existence of wetter conditions on the western side, which could be associated with greater liquid precipitation, consistent with an interaction between the prevailing westerly winds and the general N-S orientation of the island's relief. We did not detect significant differences in the availability of long-lasting snow cover during the summer, and therefore hypothesize that the main climatic difference across the two sides of the island may concern only the magnitude of liquid precipitation in summer. However, no specific precipitation data are available at this spatial scale for the island to enable testing of this hypothesis, formulated on the basis of the ecological requirements of these bank forming species.

Role of the deglaciation age of the underlying surface

The age of surfaces - the length of time the surface has been available for colonization (Fenton & Smith, 1982) - drives the extent of the ice-free areas suitable for vegetation establishment (Figs. 1, 5) and the patterns of plant colonization and succession, as well as soil development. Based on the reconstruction of the main stages of Holocene glacial evolution on Signy Island, there was a direct relationship between deglaciation age and moss bank abundance and thickness. This pattern is not unexpected, as the oldest surfaces provide a longer time available for vegetation colonization and development.

The growth rates of moss banks measured at Signy Island have not been constant over time, showing a progressive increase in recent decades: 0.6 mm/y in the pre-industrial period, 1 - 1.3 mm/y up to 1950, 2.3 mm/y between 1950 and 1980, up to 3.9 mm/y after 1980 (Fenton, 1980; Royles *et al.*, 2012; Royles & Griffiths, 2015). Applying these growth rates to our measured moss bank thickness data, we attempted to reconstruct the patterns of moss bank colonization on surfaces with different deglaciation age (Fig. 7). On this basis, on surfaces deglaciated after the end of the LIA moss bank development commenced after 1790 AD, in agreement with the findings of Favero-Longo *et al*. (2012), and showing that at least some decades are required for moss colonization after deglaciation. On surfaces deglaciated between the LIA and 6600 y BP moss banks again mainly developed after 1790, with a peak between 1950 and 1980. Surfaces with oldest deglaciation age (> 6600 y BP) also exhibited the same pattern, with almost 70% of banks becoming established after 1790, although obviously with a smaller proportion of much older banks. These data further confirm the results of the multivariate analysis (RDA) and the GLZ, that deglaciation age has not been one of the main drivers of contemporary moss bank distribution on Signy Island.

CONCLUSIONS

This study identified the main ecological requirements of moss banks in relation to environmental factors acting over different spatial scales, including topography (elevation, slope, aspect), biotic disturbance, deglaciation age of the underlying surfaces, location on the eastern vs. the western side of the island, and snow cover (as a proxy of both the possibility of direct or indirect water supply as well as of the period the ground is snow-free in summer). Moss bank abundance and distribution is the result of the interaction of multiple abiotic and biotic factors. These findings allow a better understanding of the environmental value of this characteristic feature of maritime Antarctic vegetation and provide quantitative information about their ecology. Given the uniqueness of moss banks in this region of Antarctica, it is also important to promote their conservation and protection. They face threats from a range of anthropogenic impacts including that associated with increasing tourism and logistical and scientific activities. At sites with the best development of moss banks it would be desirable to develop proposals for dedicated protected areas with access regulations. As many factors influencing moss bank distribution and abundance could be sensitive to a changing climate (Royles & Griffiths, 2015), periodic monitoring of their abundance and conservation status over, for instance, decadal time intervals is also an important practice to develop.

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Table 1. Abundance, area (m^2) and thickness (mm) of moss banks, their floristic composition, and relationship with selected biotic and abiotic factors in 2011 at Signy Island.

	Total	**<60 m**	**> 60m**
Number	310	184	126
Area range (m^2)	6.1 – 19277.2	6.34-18137	6.1-19277.2
Area median (m^2)	573.9	766.5	453.2
Area 75th quartile (m^2)	1412	1652.7	933
Thickness range (mm)	80-2100	80-2100	80-1900
Thickness median (mm)	200	200	220
Thickness 75th quartile (mm)	400	300	550
C. aciphyllum	98	56	42
P. strictum	56	31	25
Mixed stands	156	97	59
Colonized by *D. antarctica*	28	21	7
Damaged by fur seals	136	116	20
Direct snow interaction (%)	24.5	25.6	23
Indirect snow interaction (%)	9.7	10.3	8.7
No snow interaction (%)	65.8	64.1	68.3

Table 2. Abundance, area (m^2) and thickness (mm) of moss banks, their floristic composition, and relationship with selected biotic and abiotic factors in 2011, comparing the eastern and western sides of Signy Island.

	Western side of the island	Eastern side of the island
Number	144	166
Area range (m^2)	29.7-12358.4	6.1-19277.2
Area median (m^2)	877	402
Area 75th quartile (m^2)	1675	997
Thickness range (mm)	110-2100	80-600
Thickness median (mm)	410	180
Thickness 75th quartile (mm)	1000	250
C. aciphyllum	51.4	14.5
P. strictum	5.6	28.9
Mixed stands	43	56.6
Colonized by *D. antarctica* (%)	12.5	6
Damaged by fur seals	58.3	31.3
Direct snow interaction (%)	34	16.3
Indirect snow interaction (%)	12.5	7.2
No snow interaction (%)	53.5	76.5

Table 3. Main topographic characteristics relating to the partitioning (%) in terms of available elevation (m), slope (°), aspect, sectors and ice-free area (%) of the three periods of deglaciation age at Signy Island.

Deglaciation age	**> 6600 y BP**	**6600 y BP - LIA**	**Post LIA**
Available Ice-Free Area (%)	45.1	25.9	29
Available Elevation (%) **< 60 m**	64.8	50.9	25
Available Elevation (%) **> 60 m**	35.2	49.1	75
Available Aspect (%) **N, NW, NE**	43.8	39.7	31.2
Available Aspect (%) **S, SW, SE**	25.4	33	42
Available Aspect (%) **E**	8.6	8.6	15.6
Available Aspect (%) **W**	22.2	18.7	11.2
Available Slope (%) **0-10°**	39.8	49.5	45.1
Available Slope (%) **11-20°**	28.3	25.6	27.5
Available Slope (%) **21-30°**	15.9	12.9	14.5
Available Slope (%) **> 31°**	17	12	12.9

Table 4. Abundance, area (m^2) and thickness (mm) of moss banks, their floristic composition, and relationship with selected biotic and abiotic factors in 2011 in relation with the three periods of deglaciation age at Signy Island.

Deglaciation Age	**> 6600 y BP**	**6600 y BP - LIA**	**Post LIA**
Moss Bank Abundance (n)	222	75	13
Area range (m^2)	29.7-19277.2	6.1-8293	144-2928
Area median (m^2)	711	346.8	899
Area 75th quartile (m^2)	1506	903	1316
Thickness range (mm)	80-2100	100-1330	80-350
Thickness median (mm)	250	180	165
Thickness 75th quartile (mm)	525	300	200
C. aciphyllum (%)	33.4	26.6	30.8
P. strictum (%)	14.4	30.7	7.7
Mixed stands (%)	52.2	42.7	61.5
Abundance at elevation < 60 m (%)	54.9	57.3	69.2
Abundance on the eastern side (%)	47.8	62.7	100
Abundance on slopes ≤ 30° (%)	85	97.3	92.3
Direct snow interaction (%)	23.9	20	61.5
Indirect snow interaction (%)	10.4	8	7.7
No snow interaction (%)	65.7	72	30.8

Figure captions

Figure 1. Map of moss bank distribution in 2011 and of their relationship with the deglaciation age of the underlying surfaces. Legend: grey line = 60 m contour; thin grey line = 120 m contour; red line: boundary of the maximum glacial expansion at 6600 cal yr BP; blue line: boundary of maximum glacial expansion during the Little Ice Age (LIA); pale blue area: glacier boundary in 2011; black moss banks: located on the oldest surfaces (deglaciation > 6600 cal yr BP); dark grey moss banks: located on the older surfaces (6600 cal yr BP < deglaciation < LIA); pale grey moss banks: located on the youngest surfaces (deglaciation > LIA).

Figure 2. Partitioning of moss bank distribution in relation to topographic features: A) elevation (m); B) slope (°); C) aspect range (eight sectors, see Methods). Distribution with respect to the topographic features (elevation, slope, aspect) was evaluated in terms of: a) the % of population (bars), b) the absolute number of moss banks (squares).

Figure 3. Map of the distribution of moss banks relating to their species composition: pure banks of *C. aciphyllum* (grey triangle); pure banks of *P. strictum* (black rhombus); mixed banks containing both species (grey stars).

Figure 4. Partitioning of percentage of the different moss bank forming species (pure banks of *C. aciphyllum* - CA; pure banks of *P. strictum* - PS; mixed banks of both species – MIX) across topographic features: A) elevation (m); B) slope (°); C) aspect range. Legend: white columns = *C. aciphyllum*; pale grey columns = *P. strictum*; dark grey columns = mixed banks.

Figure 5 . Partitioning of the percentage of moss banks (black columns) occurring on the three classes of surfaces with different deglaciation age (grey columns).

Figure 6 . Triplot of the multivariate analysis (RDA) showing the relationship between single moss bank distribution (black dots), their characteristics (thickness, floristic composition, colonization by *D. antarctica*) and the main environmental variables representing the first two ordination axes (X1, X2, with the following eigenvalues: X1 = 0.058; X2 = 0.047).

Figure 7. Partitioning of moss bank age (colonization period AD) on surfaces of different deglaciation age (> 6600 cal yr BP; 6600 cal yr BP - LIA; post LIA).

Figure 1

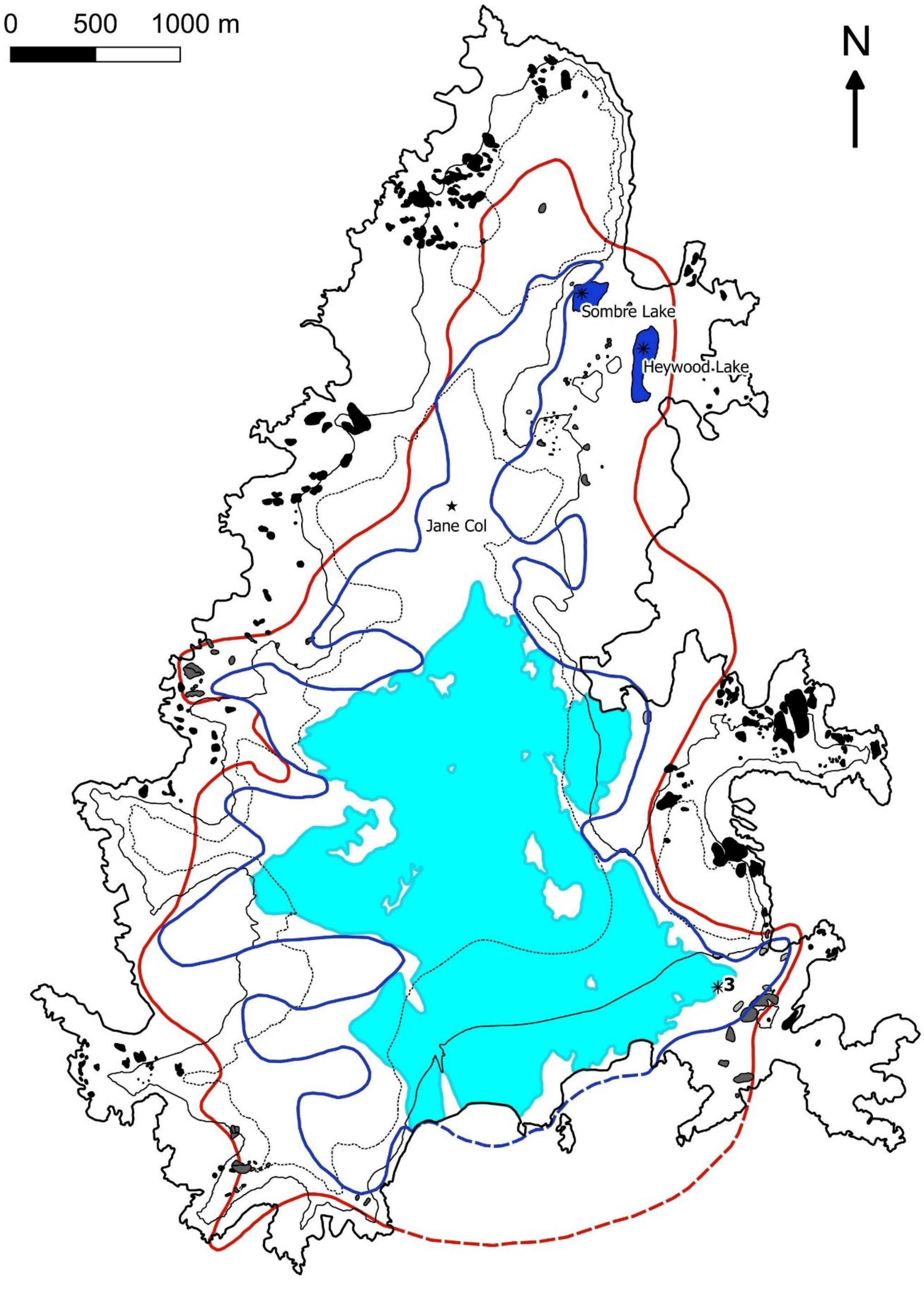


Figure 2

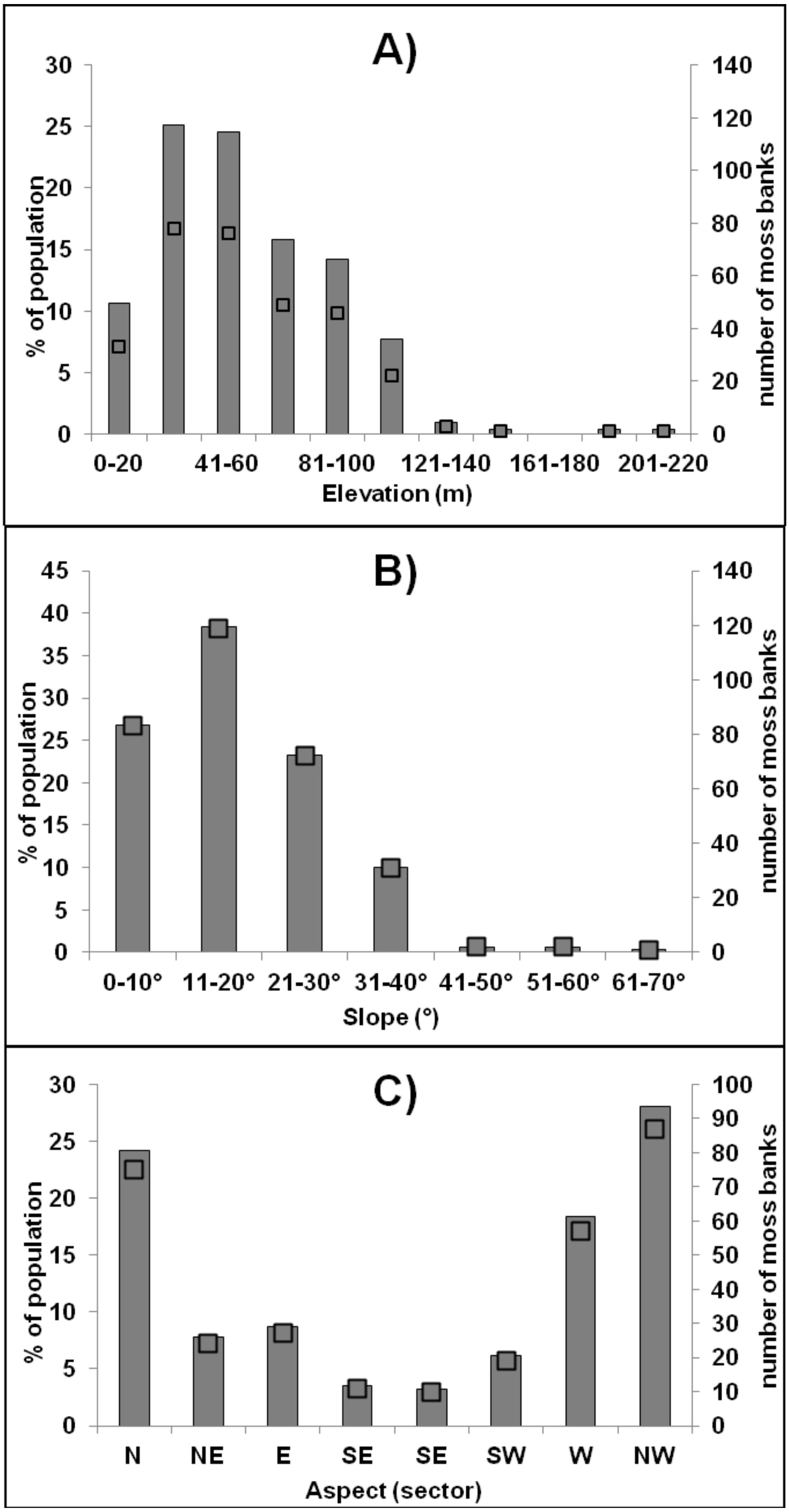

A)
% of population
number of moss banks
Elevation (m)
0-20
41-60
81-100
121-140
161-180
201-220
B)
% of population
number of moss banks
Slope (°)
0-10°
11-20°
21-30°
31-40°
41-50°
51-60°
61-70°
C)
% of population
number of moss banks
Aspect (sector)
N
NE
E
SE
SE
SW
W
NW

Figure 3

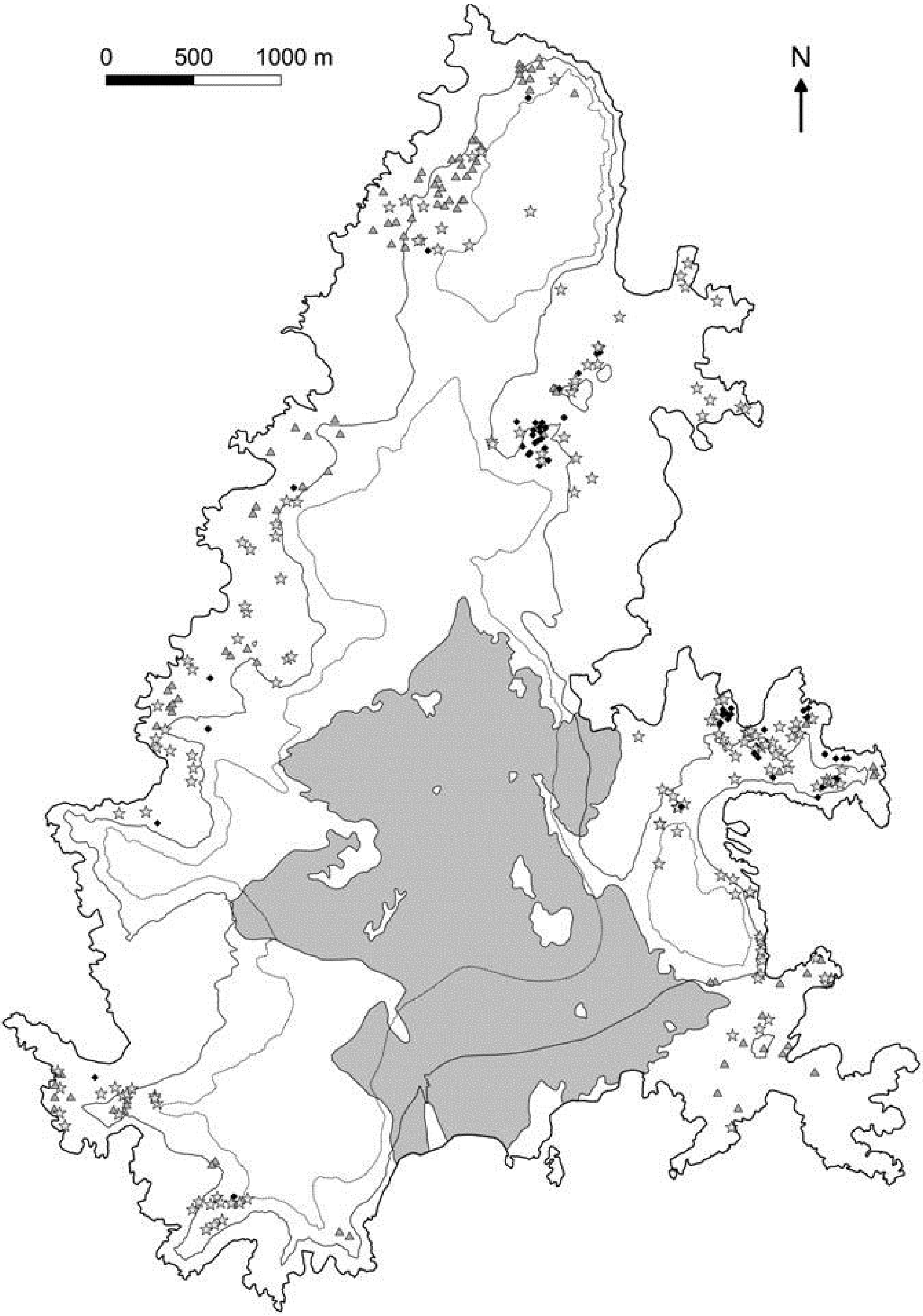


Figure 4

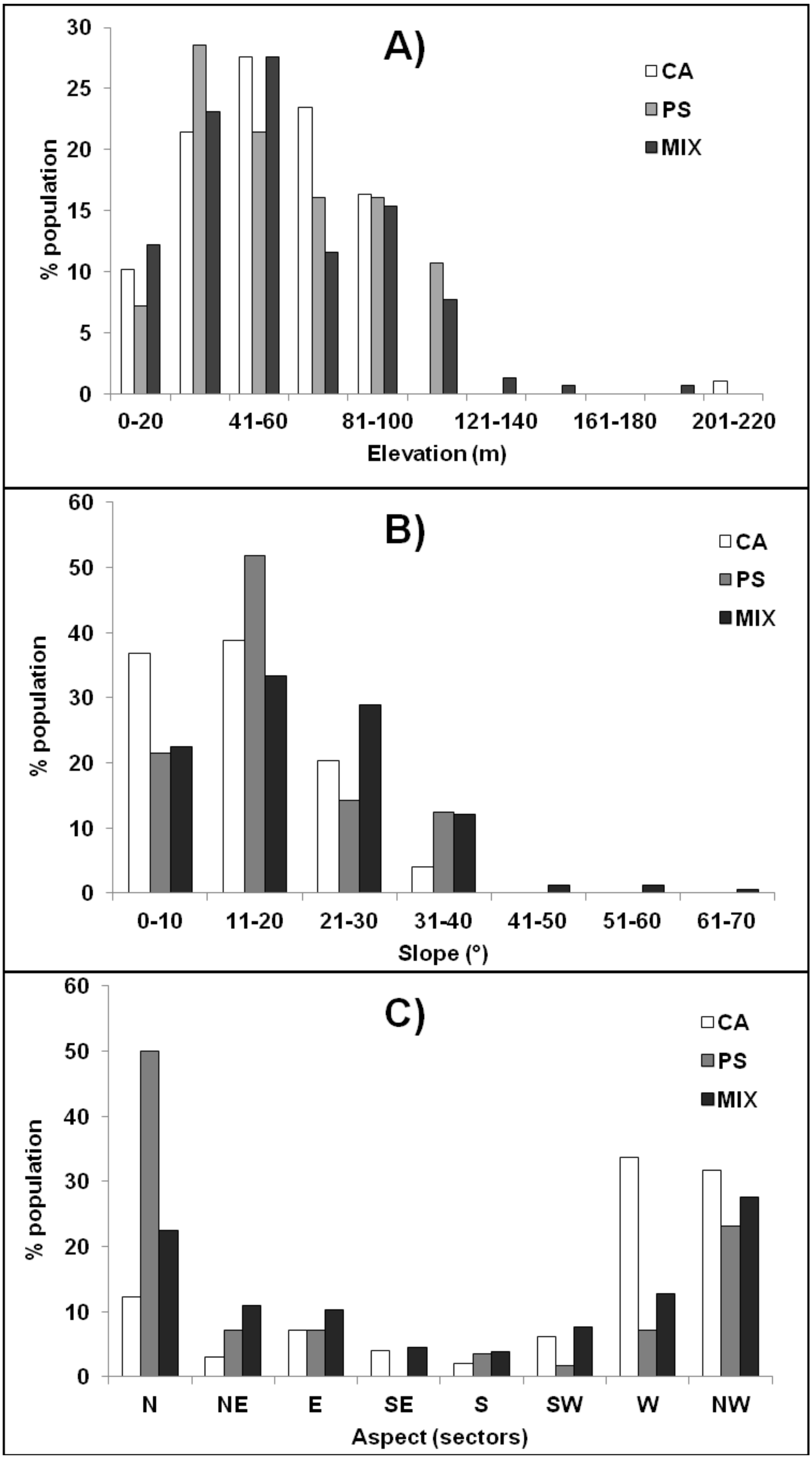

A)
CA
PS
MIX
% population
Elevation (m)
0-20
41-60
81-100
121-140
161-180
201-220
B)
CA
PS
MIX
% population
Slope (°)
0-10
11-20
21-30
31-40
41-50
51-60
61-70
C)
CA
PS
MIX
% population
Aspect (sectors)
N
NE
E
SE
S
SW
W
NW

Figure 5 ex6

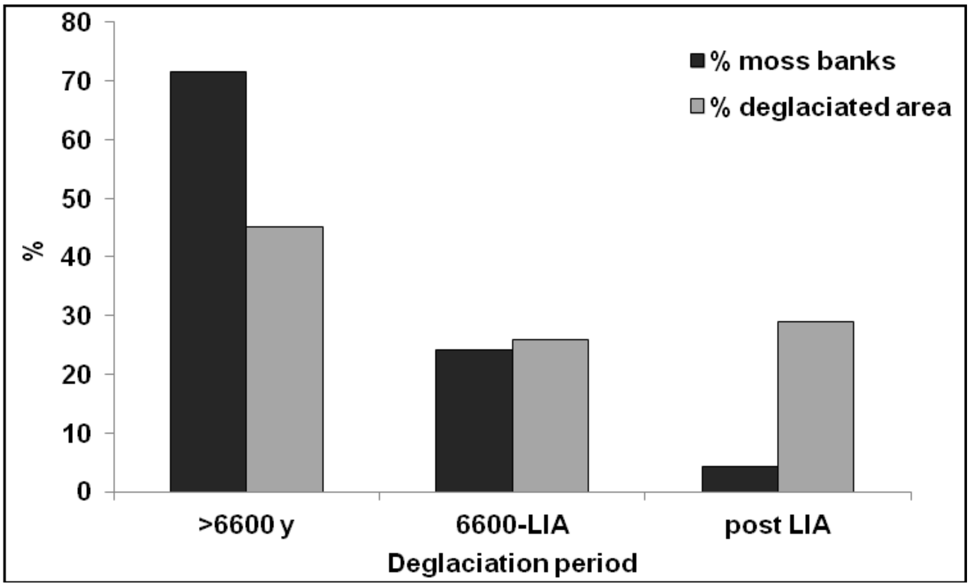

80
70
60
50
40
30
20
10
0
%
% moss banks
% deglaciated area
>6600 y
6600-LIA
post LIA
Deglaciation period

Figure 6 ex

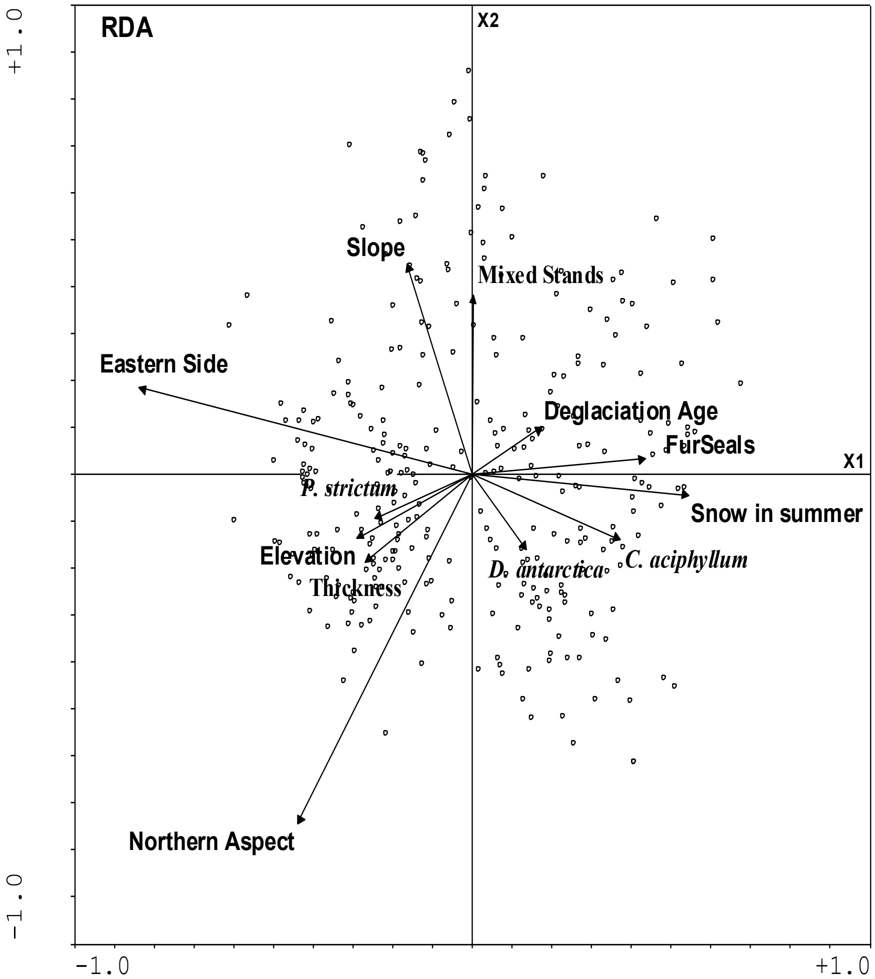
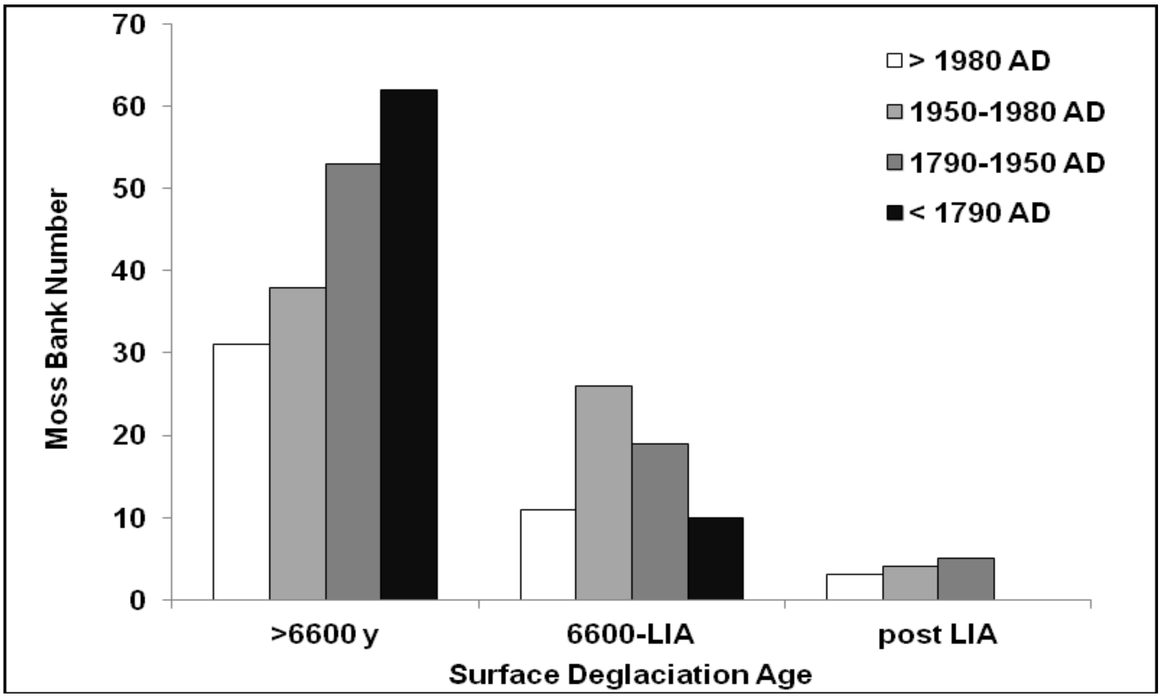

RDA
X2
X1
+1.0
-1.0
-1.0
+1.0
Slope
Mixed Stands
Eastern Side
Deglaciation Age
FurSeals
Snow in summer
P. strictum
Elevation
Thickness
D. antarctica
C. aciphyllum
Northern Aspect

Figure 7


70
60
50
40
30
20
10
0
Moss Bank Number
> 1980 AD
1950-1980 AD
1790-1950 AD
< 1790 AD
>6600 y
6600-LIA
post LIA
Surface Deglaciation Age