Original Article

Diversity and biogeography of the Antarctic flora

Helen J. Peat, Andrew Clarke & Peter Convey

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Rd, Cambridge, CB3 0ET, UK.
E-mail: hjpe@bas.ac.uk

ABSTRACT

Aim To establish how well the terrestrial flora of the Antarctic has been sampled, how well the flora is known, and to determine the major patterns in diversity and biogeography.

Location Antarctica south of 60°S, together with the South Sandwich Islands, but excluding South Georgia, Bouvetøya and the periantarctic islands.

Methods Plant occurrence data were collated from herbarium specimens and literature records, and assembled into the Antarctic Plant Database. Distributional patterns were analysed using a geographic information system. Biogeographic patterns were determined with a variety of multivariate statistics.

Results Plants have been recorded from throughout the Antarctic including all latitudes between 60°S and 86°S. Species richness declines with latitude along the Antarctic Peninsula, but there was no evidence for a similar cline in Victoria Land and the Transantarctic mountains. MDS ordinations showed that the species composition of the South Orkney, South Shetland Islands and the north western Antarctic Peninsula are very similar to each other, as are the floras of different regions in continental Antarctica. However they also suggest that the eastern Antarctic Peninsula flora is more similar to the flora of the southern Antarctic Peninsula than to the continental flora (with which it has traditionally been linked). The South Sandwich Islands has a very dissimilar flora to all Antarctic regions, probably because of their isolation and volcanic nature.

Main Conclusions The Antarctic flora has been reasonably well-sampled, but certain areas require further floristic surveys. Available data do, however, allow for a number of robust conclusions. A diversity gradient exists along the Antarctic Peninsula, with fewer species (but not higher taxa) at higher latitudes. MDS ordination suggests three major floral provinces within Antarctica: northern maritime, southern maritime and continental. Patterns of endemism suggest that a proportion of the lichen flora may have an ancient vicariant distribution, while most bryophytes are more recent colonists.

Keywords Antarctica, plant, moss, lichen, diversity, cline, biogeography, glaciation

Running title Diversity of the Antarctic flora

INTRODUCTION

Antarctica is the only continent in the world to have a macroflora that is dominated by lower plant groups, predominantly mosses and lichens with a few liverwort species and two species of flowering plants (Convey, 2001; Øvstedal and Lewis Smith, 2001). There is also a significant microbial flora including photosynthetic prokaryotes, unicellular algae, and microfungi, but these are currently not well described. Plants were first discovered in Antarctica in 1820 during Edward Bransfield's Antarctic Voyage (1819-1820), on Penguin Island in the South Shetland Islands (Anonymous, 1821, 1946). The oldest existing collection of lichens was made by an American sealing expedition in 1820-21 (Torrey, 1823), of mosses and flowering plants in 1829 by James Eights (Eights, 1833; Lewis Smith, 1981) and of liverworts by the Belgian Antarctic Expedition of 1897-1899 (Stephani, 1901). It was not until the first half of the twentieth century, however, that any major plant collections were made. A history of bryological collections is given by Ochyra *et al*. (1998) and Seppelt *et al.* (1998), and of lichens by Øvstedal and Lewis Smith (2001). Many checklists of individual areas have been published, as have taxonomic treatments of individual groups of taxa. The taxonomy and identification of Antarctic lichens is comprehensively covered by Øvstedal and Lewis Smith (2001), of liverworts by Bednarek-Ochyra *et al.* (2000) and an illustrated moss flora of Antarctica is currently in preparation.

Various schemes have been used to divide Antarctica into biological regions based on a combination of climatic and biotic characteristics (Holdgate, 1964; Pickard and Seppelt, 1984; Lewis Smith, 1984; Seppelt, 1995). Typically the Antarctic continent is divided into two zones: the first comprises the maritime Antarctic, which includes the South Sandwich Islands, Bouvetøya, South Orkney Islands, South Shetland Islands and the western side of the Antarctic Peninsula down to c. 72°S; the second comprises continental Antarctica which includes the eastern side of the Antarctic Peninsula south of 63°S, and the remainder of the continent. Lewis Smith (1984) further divided the maritime Antarctic into northern and southern regions with a boundary at 66°S, and continental Antarctica into coastal, slope and ice plateau regions. These divisions were made using fairly broad climatic or biotic features and, while there have been studies of small areas investigating whether the pattern of species' distributions follow this classification (Pickard and Seppelt, 1984), no such studies have been made for Antarctica as a whole.

In this paper we have attempted to gather together all available information on the Antarctic flora into a single database to identify how well we know the Antarctic flora, and whether any broad scale patterns in biodiversity exist. We have used a database of Antarctic plant specimens held in herbaria worldwide (Peat, 1998), supplemented with records from the Australian Antarctic Division herbarium database and species occurrences recorded in the literature, to investigate three questions:

(1) How well do we know the flora, and what important areas are there still to explore?

(2) What large scale biogeographic or macroecological patterns are displayed in the data?

(3) Do the data throw light on the evolutionary history of the Antarctic flora?

METHODS

The dataset

For the purposes of this study, we include in the Antarctic macroflora any phanerogam, bryophyte or lichen recorded from a locality south of 60° latitude or from the South Sandwich Islands (56-60°S, 26-28°W). Data on the Antarctic flora were taken from two sources: records of herbarium specimens and species occurrences cited in the literature. The Antarctic Plant Database (APD: http://www.antarctica.ac.uk/Resources/BSD/PlantDatabase/index.html) contains 31,909 records of specimens collected south of 60°S and held in over 50 herbaria worldwide (Peat, 1998), together with 1262 records from the South Sandwich Islands. This database was supplemented with 3346 Antarctic records from the Australian Antarctic Division's herbarium (ADT) database. In addition, a database of literature records was constructed to hold species identifications where a collection locality was listed; this added 2,728 records from 71 publications. To avoid duplication of data, publications citing records of specimens that are listed in the Antarctic Plant Database were not included in the database of literature records

Bouvetøya (54°25'S, 3°18'E), while generally included in the maritime Antarctic, was not included in our data set because of the very limited botanical collections from this island (Engelskjøn, 1986a). No attempt was made to critically assess specimen determinations but, wherever possible, current nomenclature has been used and the latest name is used for any known synonyms. The identification of many specimens in the British Antarctic Survey Herbarium (AAS) has recently been checked by D. Øvstedal during the development of the

Antarctic lichen flora (Øvstedal and Lewis Smith, 2001) or by R. Ochyra as part of the ongoing development of an illustrated moss flora of Antarctica. However, lichen specimens determined by C. W. Dodge that have not subsequently been redetermined, and any checklists written by Dodge, have not been included in the biodiversity analyses; this is because many of the species described by Dodge are no longer accepted as valid (Castello & Nimis, 1995). Whilst the type specimens described by Dodge have been re-examined, we feel it is unlikely that use of the resulting synonyms would give reliable identifications for non-type material. Statistical analyses whose use requires data on the number of specimens were performed using only herbarium specimen data, as checklists given in the literature do not consistently record the number of specimens of each species that were collected.

Ice-free areas

The area of land potentially available for plant colonisation was taken from the ungeneralized layer of the Antarctic Digital Database (ADD Consortium, 2000), a topographic database that includes the area of sea, ice, rock, lake, shelf and moraine. The rock areas were computed by summing the areas within boxes of one degree latitude and longitude and include all such areas greater than 1000 m^2. There will be systematic errors of less than 1% in the total areas recorded caused by the map projection, and unknown errors deriving from incomplete data (for example, rock outcrops that cover too small an area to be represented in the ADD). Overall, however, we believe these errors to be small and their impact on diversity and biogeography patterns to be negligible.

Biodiversity analyses

Species richness measures were calculated for defined geographical areas (Fig. 1) and latitude bands. For the maritime Antarctic these areas were based on a subdivision of the Antarctic Peninsula into northern and southern sections, with the southern section itself divided into east and west areas, separate consideration of Alexander Island and the nearby mainland coast, and also of three major island groups (South Shetland Islands, South Orkney Islands and South Sandwich Islands). These areas were based essentially on the long-established climatic and biotic zones (Lewis Smith, 1984). The Antarctic continent was divided arbitrarily into a series of well-established sectors (Greene *et al*., 1970), defined solely by longitude, the aim of which was to investigate possible spatial heterogeneity in plant diversity and assemblage composition within the continent. Abundance information was not used because of the non-quantitative nature of sampling at most locations. Areas either close to scientific stations or that are relatively easy to access have typically been sampled more often and more comprehensively than remote or less accessible sites. Many of the latter will have been visited only once, often by a non-specialist. In addition to examining richness estimates at the species level, these were also calculated at higher taxonomic levels (genus, family, order, class) to identify whether any patterns exhibited at the species level were also apparent for higher taxonomic levels. To test whether any patterns in species richness and latitude were being caused by sampling bias we calculated two further estimates of species richness, Chao2 and Jacknife1 (Magurran, 2004). These were chosen because they showed the least overall bias (Chao2) and greatest accuracy (Jacknife1) in a recent review of species richness estimators (Walther & Moore, 2005). Values were calculated using EstimateS version 6.0b1 (Colwell, 2001) with a sample being defined as all specimens collected by an individual collector within one season. As information was required on the collector and date of collection only herbarium data were used for these analyses.

Biogeographic patterns were examined using multivariate methods in PRIMER (Plymouth Routines in Multivariate Ecological Research version 5 and beta-test version 6, Primer-E Ltd, Plymouth Marine Laboratory, UK; Clarke and Warwick, 2001). Species records were classified into areas in two ways: firstly by latitude band, but separating Antarctic Peninsula and non-Antarctic Peninsula records, and secondly into predefined areas (Fig.1). As these areas are of different sizes and sampling effort in each was very dissimilar, only presence/absence data were used in the analyses. Similarities between the different areas based on species co-occurrences were calculated using the Bray-Curtis coefficient, and multi-dimensional scaling (MDS) ordinations then plotted.

To determine whether there were subtle patterns in taxonomic composition we calculated the taxonomic distinctness index of Clarke & Warwick (1998). This index calculates the average taxonomic distance between randomly chosen pairs of species within the assemblage. To determine whether the value is significant or not, this value is compared with the mean value for assemblages of the same number of species but selected at random from the entire Antarctic plant species list for that group (mosses or lichens). These confidence intervals are broader for smaller richness values, giving the plots a characteristic funnel shape. All known Antarctic moss and lichen species were used as the master list and each sorted into a taxonomic hierarchy. Mosses were classified into families, orders and classes using Buck & Goffinet (2000), and lichens, similarly, using Eriksson *et al.* (2001). Not all lichens could be assigned to a family or order in this classification, and in such cases the species were assigned a unique “dummy” value for the unknown taxon. Liverworts and vascular species were excluded from some of the biodiversity analyses because there are very few Antarctic species. There are only two species of vascular plant, both of which occur on the western side of the Antarctic Peninsula and other maritime Antarctic archipelagos (Lewis Smith, 2003). The majority of the 25 liverwort species (Bednarek-Ochyra *et al.*, 2000) are also restricted to this area with only eight species found at latitudes greater than 65°S on the Antarctic Peninsula, and a single species found elsewhere in Antarctica.

RESULTS

How well has the Antarctic flora been surveyed?

The traditional view of Antarctica, one of a largely unvisited wilderness almost unknown to science, is quite misleading. Whilst collection of plants has been sporadic and some of the more remote areas have received single or very few repeat visits (and none by specialists), Antarctica is far better known biologically than is often realised. Nevertheless, the question of sampling effects and bias on studies of biogeography and biological diversity is a very real one. To assess the extent of sampling for macroflora, we compared areas that have the potential for plant colonisation (*i.e.* areas of ground free from permanent ice) with areas from which plants have been recorded. Figure 2 collates one degree boxes which contain areas of ice-free land. In all, 914 boxes include some ice-free ground, and plants have been collected in 276 (30%) of these. This analysis, however, may underestimate the total percentage of ice-free ground from which plants have been sampled, as the total area of ice-free ground in boxes without plant records is 2.2828×10^4 km^2, whereas the total area of ice-free ground in boxes with plant records is 2.2727×10^4 km^2 (49.9%). It is not known how many boxes have been visited with no plant life being observed, so it is impossible to distinguish between those that have not been visited from those in which no plants have been recorded.

To assess geographic variations in sampling effort, records were pooled by geographic area (Table 1). This reveals that, as would be expected, some areas have been very well studied, while other areas have received much less attention. In particular the South Shetland Islands, where there are 10 permanent scientific stations and many more summer-only operations and refuges, has been particularly well studied. There are, however, at least 1800 records (including both herbarium and literature records) from all areas except the Maud and Byrd Sectors of the continent. Byrd sector contains no permanent research stations and has been little explored biologically other than during the American expeditions to Marie Byrd Land in 1934 (Siple, 1938) and 1940-41, and a few collections made by geological and glaciological parties working on Thurston Island and the Eights Coast. There are a number of coastal stations in Maud Sector, but much of the ice-free ground here is at high altitude and difficult to access. However, plant collections have been made in Dronning Maud Land and at the Schirmacher Oasis (*e.g.* Engelskjøn, 1986b; Richter, 1995) and the small number of records is probably a true reflection of the paucity of plant life in these areas.

It is a well-established feature of biodiversity studies that the observed taxonomic richness of a region is a strong function of the sampling intensity, as described in broad terms above for Antarctica. The quality and thoroughness of sampling, and of the subsequent taxonomic work, is also important, but this cannot always be assessed from literature records. The herbarium records in the Antarctic Plant Database have, however, been verified thoroughly. We therefore tested the potential impact of sampling heterogeneity for Antarctica as a whole by determining the relationship between the number of specimens collected and the number of species recorded for all one degree lat/long boxes. As would be expected there was a strong positive correlation between the number of specimens collected from a given box and the plant species richness recorded for that box (Fig. 3a). As these boxes are of different physical area depending on latitude, and contain differing amounts of ice-free ground, we also investigated the relationship between ice-free area and the number of species within each box (Fig. 3b & 3c). These analyses illustrated that within continental Antarctica (here defined as all latitudes with longitudes clockwise between 47°W and 80°W plus all localities further south than 75°S) there was no discernable relationship between the area of ice-free ground within a box and the number of species recorded from that box (Fig. 3c).

Within the Antarctic Peninsula, boxes containing large areas of ice-free ground show great variation in the number of species that have been recorded from them. However, large numbers of species have not been recorded from boxes containing smaller areas of ice-free ground, giving an indication that the area of ice-free ground may set an upper bound to the richness of plant assemblages in that box (Fig. 3b). The regression line of this upper bound was calculated using the method of Blackburn *et al.* (1992) and splitting the data into eight equal sized bins. It was found to be:

$$\log_{10} S = 0.782(\log_{10}A) + 0.663 \ (R^2 = 78.3\%),$$

where S = number of species and A = area. The slope of this upper bound relationship could be taken as an estimate of the scaling coefficient (traditionally designated z) of a species-area relationship for Antarctic plants (Brown, 1995). The raw data represent independent areas and hence are closer to an individual island plot than a series of nested samples, but the estimate, z=0.78, is higher than reported typically for floras at a scale below that of biogeographic provinces (Rosenzweig, 1995).

Diversity Patterns

a. latitudinal gradients

There are two areas within the Antarctic where geographical continuity may permit the existence of latitudinal and, implicitly at least, environmental gradients. These are the Antarctic Peninsula and linked archipelagos (60°S-77°S), and in the Ross Sector of the continent, from Cape Hallett southwards along the Victoria Land coast and then south through the Transantarctic Mountains (69°S-86°S). The Prince Charles Mountains (Enderby Sector) might allow a similar test but they extend over a smaller range of latitude (69°S to an isolated peak at 76°S) and have yet to be systematically surveyed by botanists. To identify any influence of these gradients on diversity, plots were made of the number of species recorded at each degree of latitude within each (Fig. 4). These suggest that a diversity gradient exists along the Antarctic Peninsula but no such gradient is apparent through Victoria Land and the Transantarctic Mountains. The diversity gradient along the Antarctic Peninsula is clearest for lichens, with a strong cline in species richness from 62°S to around 70°S. However, for mosses, although there is a general southwards decline in species number, this decline is not even, and richness remains broadly constant between 63 and 65°S and again between 69 and 71°S.

The nature of the gradient along the Antarctic Peninsula was investigated further by plotting the percentage of species whose most northerly record occurs within each latitude box (Fig.

5). This shows that the majority of species recorded from along the Antarctic Peninsula have their most northerly record between 60 and 62°S, and very few species have been collected solely at more southerly latitudes. This indicates that the diversity cline is driven by increasing numbers of species being lost from the assemblage with increasing latitude, rather than taxonomically different assemblages being found at different latitudes. In other words, the diversity gradient is driven almost completely by decreasing local (alpha) diversity with increasing latitude, and the contribution of turnover (beta) diversity is small. To investigate whether the gradient was caused by the loss of individual species or by the loss of whole groups of species at higher taxonomic levels, the numbers of species, genera, families and orders at each latitude band were quantified (Fig. 6 a,b). This shows that, while a taxonomic diversity gradient is evident for genera, at higher taxonomic levels it becomes less obvious, particularly at latitudes beyond 70°S, and suggests that the gradient is principally caused by loss of species and genera rather than higher groups (families, orders or classes) with increasing latitude.

To test whether these clines in observed richness were driven by a decline in sampling intensity towards higher latitudes, we calculated two univariate estimates of species richness that are least biased by sampling error, Chao2, or the most accurate, Jacknife1 (Walther & Moore, 2005). These measures are plotted alongside observed species richness (Fig 6 c,d), and suggest strongly that the observed cline is real. An alternative procedure to correct for variation in sampling intensity is to use the residual about the regression line fitted to the relationship between observed richness and sample number (Fig. 3a). A positive residual indicates a grid box with a relatively large species richness given the number of samples in that box, and a negative residual, a correspondingly low, species richness (Clarke & Lidgard 2000). For the Antarctic plant data (Fig. 3a) a quadratic regression was a better fit than a linear model, and for the Antarctic Peninsula the residuals showed a statistically significant inverse relationship with latitude ($P<0.009$). We conclude that the cline in observed richness along the Antarctic Peninsula is real, being robust to a range of methods to correct for the effects of sample bias.

b. patterns in biodiversity

The MDS ordinations using the predefined areas (Fig. 1) show that the patterns found for mosses and lichens are somewhat different (Fig. 7a & 7b). The lichen pattern shows 3 distinct clusters – (i) the South Orkney and South Shetland Islands and the northern and western Antarctic Peninsula; (ii) the eastern and southern sections of the Antarctic Peninsula; and (iii) Eastern Antarctica. The Scotia sector (not including the Antarctic Peninsula) and the South Sandwich Islands are outliers. Cluster analysis confirmed that these groups were significantly different from one another ($p< 0.05$). The MDS ordination for mosses is more diffuse, but the plot for the Antarctic Peninsula areas matches well with the geographic positions of these areas, although the eastern side of the Antarctic Peninsula is shown to be distinctly different from the western side. The South Sandwich Islands are once again very different from all other localities and Byrd Sector is distinctly different from the other sectors in continental Antarctica. As the geographic areas used in this analysis were, of course, chosen *a priori*, we therefore chose also to look at the Antarctic Peninsula in more detail using latitude bands rather than areas (Fig. 7c & 7d). In these analyses the patterns for mosses and lichens are more similar, with the MDS ordination in both groups broadly mirroring the latitudinal gradient. In both groups, however, there is a suggestion of a division into low latitude (60°S to about 71°S) and high latitude, continental, groups (above 71°S or 72°S). This analysis thus supports the traditional division of the Antarctic terrestrial flora into Antarctic Peninsula (with associated island groups) and continental assemblages. The MDS ordination also suggests a finer scale differentiation of the floras of the Antarctic Peninsula, and this is discussed in more detail below.

c. Taxonomic diversity

The biogeographic patterns shown in Fig. 6a,b suggest that the assemblage composition of the Antarctic Peninsula flora in terms of higher taxa (families, orders and classes) is fairly independent of latitude. The taxonomic distinctness values within different Antarctic regions are shown in Fig. 8. There is no evidence for any trends in taxonomic distinctness values with increasing latitudes along the Antarctic Peninsula, supporting the results shown in Fig. 6a,b. The plot for mosses (Fig. 8a) shows that at many of the Antarctic Peninsula latitudes the assemblages have distinctness values that are larger than expected (that is they lie above the upper 95% confidence interval), whereas roughly half the latitude bins for Eastern Antarctica have significantly low distinctness values. This indicates that, for most of Antarctica, the moss flora is not simply a random assortment of the total regional species pool. Species from a wide variety of higher taxa are found in the Antarctic Peninsula region whereas in continental Antarctica there is a restricted species pool representing very few of the higher taxa. The pattern for lichens is quite different (Fig. 8b). Here, assemblages from the Antarctic Peninsula all fall within the 95% confidence intervals, whereas the continental sample still has many latitudinal bins with significantly low distinctness values. Current uncertainties in the higher classification of lichens, however, make it difficult to interpret these results with confidence.

DISCUSSION

Prior to discussing any of the patterns in the diversity and biogeography of the Antarctic flora it is essential to be reasonably confident that enough sampling has occurred, in sufficient localities, to ensure that any patterns proposed are a result of species' distributions and not determined solely by patterns in collecting. It can be seen from Fig. 2 and Table 1 that species have been recorded from a wide variety of Antarctic locations and that there are no major regions from which no plants have been recorded. Specimens have been collected from all latitudes between 60°S and 86°S, and at a good range of circumpolar localities. There are, however, smaller regions that warrant further botanical investigation, including the Byrd sector (100-140°W), the southern extremes of the Antarctic Peninsula, the Transantarctic Mountains in the Ross Sector (particularly at latitudes beyond 80°S) and some areas in the Maud and Enderby sectors.

Although it is undoubtedly true that, as with many areas of the world, continued work by experts will add new records or revise existing taxonomies, we believe that the broad patterns we detect are real. Plant specimens have been collected by more than 500 individuals over a period of more than 160 years, so it is unlikely that the collecting patterns of either particular individuals or research expeditions will have any significant effect on the overall biogeographical patterns. There is nevertheless a strong relationship between number of specimens collected in a given one-degree box and the number of species recorded for that box (Fig. 3a). This is to be expected as botanists will tend to concentrate their efforts in the most interesting and diverse habitats, and there are also strong indications that the recorded plant species richness is highest in those areas easily reached from long-established research stations. This is partly because both plant assemblages and research stations need areas of ice-free ground, but it also reflects the well-known 'field station hot-spot' effect. There is also the inevitable bias that the more isolated areas, requiring greater logistic support, will have been less visited by either botanists or casual collectors. In addition, genuine biogeographic variability will be introduced by differences in historical processes (for example the time for which bare ground has been exposed to colonisation following glacial retreat or changes in relative sea level).

The area of ice-free ground was not found to be a strong determinant of the number of species found in different localities, at least when studied at the spatial scale of 1 degree boxes of latitude and longitude (Fig. 3b, c). This is not surprising as many of the larger ice-free areas are in exposed, high altitude sites where plant life is restricted by the extreme temperatures and low water availability (particularly in continental Antarctica), or have only recently been exposed to colonisation by retreating ice or changes in sea level. The richest plant communities tend to be found at low altitudes in coastal regions, particularly where there is a diverse range of habitats. Signy Island, in the South Orkney Islands, for example, while a fairly small island (c. 25 km^2) has a wide range of topographical and geological variations, which are snow-free for at least three months of the year, and a relatively high air temperature because of the ameliorating effects of the surrounding ocean (Lewis Smith, 1972). It has the richest moss (at least 65 species) and lichen floras (220 species) in the Antarctic (Ochyra, 1998, Øvstedal and Lewis Smith, 2001), though it has also been a centre of terrestrial ecological research since the early 1960s. For the Antarctic Peninsula and surrounding islands, there is an indication that the area of ice-free ground may set an upper bound on assemblage richness (Fig. 3b). Two factors could be at work here. The first is that larger areas of ice-free ground are likely to support more diverse plant assemblages. The second is that a gradient in temperature along the Antarctic Peninsula means that more northerly boxes are likely to contain a higher percentage of ice-free ground, and this may combine with a cline in plant diversity along the peninsula to produce the pattern observed. As so often with ecology, it is difficult to separate these various influences. The upper bound regression line, however, may be a useful predictor to estimate the limits to increases in species richness in the Antarctic Peninsula where rapid regional climate change is causing ice recession and an increase in ice-free areas.

Biogeographic areas within Antarctica

Multivariate analyses using multi-dimensional scaling (Fig. 7) suggest that the traditional division of the Antarctic terrestrial flora into maritime and continental regions may be too simplistic, and further subdivisions may be necessary to represent all phytogeographic zones. Lewis Smith (1984) divided the Antarctic into two geobotanical regions (Maritime and Continental) and further subdivided these into two and three provinces respectively. The Maritime Antarctic was divided into northern and southern provinces, with the west coast of the Antarctic Peninsula to c. 66°S and associated islands (South Orkney, South Shetland and South Sandwich Islands) in the northern province and the west coast of the Antarctic Peninsula from c. 66°S and the north-east coast of the Peninsula to c. 63°S in the southern province. Continental Antarctica was divided into three zones: coastal, which included the east coast of the Antarctic Peninsula, and the coastal fringe of Eastern Antarctica and Western Antarctica south of 70°S; the slope zone, which included the mountain and glacier zone inland from the coast; and the ice plateau zone, comprising of the central ice plateau on the interior of the continent. Our MDS ordinations, however, suggest that some alterations of the definitions of the provinces are required if they are to represent justifiable phytogeographical zones. We suggest a division into two regions, with a finer-scale division into three provinces (Table 2). The two regions, maritime and continental, are clearly revealed by the MDS ordination, with the boundary occurring at ~72°S. However, more detailed work suggests a finer-scale division of the maritime region into two provinces, with the boundary lying between the western coast of the Antarctic Peninsula at ~68°S and the eastern coast at ~65°S. In an analogous consideration of Antarctic biodiversity patterns based largely on terrestrial fauna, Chown and Convey (in press) propose a biogeographical boundary (the “Gressitt Line”) with analogous strength to the Wallace Line of south-east Asia, situated in a closely similar position to the maritime – continental boundary proposed here.

The South Sandwich Islands are generally included as part of the maritime Antarctic region, whereas our analyses indicate that the moss and lichen floras are distinctly different from those elsewhere on the Antarctic Peninsula. The number of lichen species recorded from this archipelago is very low (46 species, Øvstedal and Lewis Smith, 2001) but most of the lichens which have been collected there also occur elsewhere in the maritime Antarctic and, indeed, many are otherwise endemic to the Antarctic (Convey *et al.*, 2000; Øvstedal and Lewis Smith, 2001). Further studies in the region are needed to determine whether the lichen flora is truly impoverished resulting from the fairly recent geological age of the islands (1-3 Myr, Holdgate and Baker, 1979) and their extreme isolation or, rather, due to the paucity of botanical studies. There have been only two comprehensive botanical studies of the islands in 1964 (Longton & Holdgate, 1979) and 1997 (Convey *et al.*, 2000). The number of lichens recorded rose from 16 in the first study to c. 45 in the second, so further collecting in the region is likely to yield more species. The moss flora is proportionally much richer (38 species), and unusual in that many of the mosses are found only, or predominantly, on heated ground around fumaroles (Convey *et al.*, 2000). A number of species not recorded elsewhere in the Antarctic have been found here, whose presence is likely to be due to long distance dispersal of these species from sub-Antarctic South Georgia and more distant continents, especially South America. Other areas in the Antarctic where geothermally influenced soils are present, such as Deception Island (Lewis Smith, 2005a,b), and Mts Melbourne and Erebus (Skotnicki *et al.*, 2001) in Victoria Land, also have unusual bryofloras. In such sites the increased temperatures and water availability allow the establishment of species which otherwise would not survive. Further MDS ordinations, including the species found on South Georgia and other sub-Antarctic islands, are necessary to determine whether the South Sandwich Islands should be considered part of the northern Maritime Antarctic, the sub-Antarctic or as sufficiently distinctive to justify their own province.

The eastern coast of the Antarctic Peninsula is traditionally classified with continental Antarctica, based mainly on its harsher climate compared with the western coast. However, MDS ordinations indicate that the eastern Antarctic Peninsula has more in common, in terms of species composition of the flora, with the south-western Antarctic Peninsula than to any of the truly continental Antarctic regions. We therefore suggest that the eastern Antarctic Peninsula should form part of the southern Maritime region and that the boundary between the northern and southern provinces should be further south at 68°S, rather than 66°S as suggested by Bednarek-Ochyra *et al*. (2000). Based on the MDS ordinations we have also included the northeast Antarctic Peninsula to 65°S in the northern province rather than the southern one (Table 2).

While our analyses do confirm that most continental areas outside the Antarctic Peninsula have broadly similar floras, further botanical investigation is required in order to confirm whether the southern portion of the Scotia sector of continental Antarctica is more appropriately linked northwards with the southern end of the Antarctic Peninsula or to the other continental Antarctic regions. Furthermore, whilst the lichen flora of the adjacent Byrd sector is similar to the other continental sectors, the moss flora is more dissimilar. Only ten moss species have been recorded from this region and two of these (collected from islands off the Eights Coast, 72°S 90-100°W) represent species otherwise found only in the maritime Antarctic (*Andreaea gainii* Cardot and *A. regularis* Müll. Hal.). Further exploration of the area around the Eights Coast should help determine whether this region more accurately should be considered as the extreme southern extent of the maritime Antarctic.

Latitudinal gradients in plant diversity within Antarctica

There have been many cited examples of latitudinal gradients in taxonomic diversity (reviewed by Gaston & Williams, 1996). There have also been suggestions of latitudinal gradients in the diversity of the Antarctic flora (*e.g.* Convey, 2001; Green & Broady, 2001; Clarke, 2003; Kappen, 2004), but the evidence cited usually combines diversity data from sub-Antarctic islands with that from the Antarctic continent, which is a much wider area than in our study. In this study we have examined two regions within Antarctica *sensu stricto* where habitat area runs meridionally, to determine whether there is evidence for the existence of latitudinal gradients in diversity. These analyses confirm that the Antarctic Peninsula shows a decline in the number of lichen, moss and hepatic species with increasing latitude (Fig. 4), a pattern which is robust to corrections for the effect of sample size (collection intensity, Fig. 6 c,d). Some intermediate latitudes also have particularly low numbers of species, but these are likely to be a direct function of a lack of ice-free areas. For instance, the only land areas at 61°S are the northernmost islands in the South Shetland Islands (Elephant Island, Gibbs Island and Clarence Island), whose true diversity may also be underestimated as few collections have been made from these isolated islands. Likewise, around 66°S, other than a few offshore islands much of the coastline is steep and glaciated. There is much less evidence for a diversity gradient when examined at the level of family or above, at least at far south as 71°S, after which the number of higher taxa found drops off rapidly (Fig. 6 a,b)

This finding is supported by analyses using taxonomic distinctness measures (Fig. 8 & 9). The data for mosses show that not only are there more moss species on the Antarctic Peninsula than in other Antarctic regions but also that the Antarctic Peninsula is more diverse taxonomically. However, there is no evidence for a cline in taxonomic distinctness (as against species richness) along the Antarctic Peninsula. The taxonomic distinctness values for lichen species show less differentiation between the Antarctic Peninsula and continental localities, and no areas have significantly high values, while some areas in eastern Antarctica, and at 64 and 65°S on the Antarctic Peninsula, have particularly low distinctness values. Again, however, there is no evidence of any significant variation in taxonomic distinctness with latitude. The gradient in the number of species is therefore not caused because whole groups, such as families, are unable to survive at higher latitudes, but because individual species have either not colonised that far south or have not adapted to the harsher climatic conditions. Further investigation is required to attempt to determine why some species are found at southerly locations but other closely related species are not. Many factors may be important such as growth form, availability of propagules and life history (Longton, 1988).

There is currently no evidence for a diversity gradient along the Victoria Land coast and into the Transantarctic Mountains (Fig. 4) although there have been very few collections made at some latitudes, and the number of species recorded may be heavily biased by collections made close to the Italian, American and New Zealand research stations in this region. There have been no recent botanical surveys south of the McMurdo Dry Valleys, although there are unpublished anecdotal reports from New Zealand workers of high lichen diversity (around 27 species) in the vicinity of Mt Kyffin (83° 45'S) on the southern edge of the Beardmore Glacier (Tuerk, R., SCAR Open Science Conference, Bremen, July 2004). This observation greatly strengthens our preliminary finding of no marked cline in macrofloral diversity along the Transantarctic Mountains in Victoria Land. The New Zealand Antarctic Programme is currently leading the Latitudinal Gradient Project, which involves studying both physical and biological features, including the biodiversity of terrestrial organisms, at a number of sites along a gradient on the Victoria Land Coast from 72-86°S (Peterson and Howard-Williams, 2001). The data collected from this project should help provide a more representative dataset with which to investigate the existence of any latitudinal gradients in Victoria Land to match that detected along the Antarctic Peninsula.

Historical aspects

The majority of Antarctic flora is generally thought to have originated fairly recently with recolonisation following the retreat of glaciers and ice-sheets from their Pleistocene maxima (Hertel, 1987, Galloway 1991, Ochyra *et al.* 1998), predominantly through long-distance dispersal with wind as an important vector (Muñoz *et al.* 2004). What is unclear, however, is how many species survived the Pleistocene glaciations on ice-free nunataks and oases. In the maritime Antarctic all low altitude, coastal regions are believed to have been obliterated by much expanded glaciers and ice sheets during the last glacial maximum (LGM) (Larter and Vanneste, 1995; Ó Cofaigh *et al.*, 2002; COHIMAR/SEDANO Scientific Party, 2003; see also reviews placing these studies within a biological context by Convey, 2003, and Chown and Convey, in press), and only re-exposed as ice has retreated over, at most, the last 10,000 years. While recent biogeographical studies do indicate that this view must be overly simplistic and inaccurate at small scales (Pugh and Convey, 2000; Maslen and Convey, in press), it remains the case that no potential refugia can be proposed in coastal areas of this region based on current glaciological reconstructions.

In the coastal continental Antarctic, it is now clear, from palaeolimnological data that some coastal oases have hosted terrestrial or freshwater faunas for up to 150,000 years (Hodgson *et al.*, 2001; Squier *et al.*, 2005), and hence that at least some terrestrial habitats have a considerably longer continuous history of exposure extending well beyond the LGM. However, these findings still fall a long way short of demonstrating persistence throughout the Pleistocene. Elsewhere in the continental Antarctic, diverse studies of the glaciology and limnology of the Victoria Dry Valley region (Denton et al., 1993) and most recently the molecular biology of terrestrial arthropods (Nolan *et al*. in press; Stevens *et al*. in press; Stevens & Hogg, in press; Stevens & Hogg, 2003) support the existence of terrestrial and freshwater habitats throughout the Pleistocene and back to, at least, 1-2 million years ago if not the Miocene glaciations of 3-5 million years ago.

That a general historical explanation may not apply to the Antarctic macroflora as a whole is indicated by the very different patterns of endemism in Antarctic mosses and lichens. Øvstedal & Lewis Smith (2001, 2004) report 130 endemic lichens from a total Antarctic flora of 393 species (a level of endemism of 33% - 50% in continental Antarctica), whereas only 6-7% of mosses are currently believed to be endemic (Ochyra *et al*. 1998) and none of these are endemic to continental Antarctica. Whilst these endemism figures are likely to be affected by improved studies of the Periantarctic islands, and detailed comparisons of Antarctic specimens with those from nearby southern hemisphere locations, they do suggest that, at a high taxonomic level, the two dominant groups of plants have fundamentally different evolutionary histories in Antarctica. In particular, they suggest that the bryophytes are (almost) entirely more recent colonists, while the lichens may include a component with a more ancient and vicariant distribution. This lichen pattern is also noted in elements of the invertebrate fauna of some inland nunataks, including mites (Marshall & Pugh, 1996) and tardigrades (Convey & McInnes, 2005). The recent origin for much of the flora is supported by species richness patterns with the highest number of species occurring in localities closest to neighbouring continents and where there are more favourable climatic conditions for establishment. It is certainly clear that Antarctica experiences a continuous, if low level, input of propagules from the other Southern Hemisphere continents (Marshall, 1996). Any individual colonising propagule faces many obstacles during the dispersal and colonisation processes, requiring long distance transfer, arrival in a suitable area of habitat at a suitable time of year, and acquiring the resources necessary for both initial survival and long term establishment (Clarke, 2003). However, it is also clear from many culture and environmental manipulation experiments that propagules can remain dormant and viable in propagule banks in soil and (probably) ice for considerable periods (Lewis Smith 1993; During, 1997). Such abilities have important implications for future changes in diversity to be expected under current trends of climatic change in parts of Antarctica (Convey, 2003).

It is difficult, however, to draw conclusions about the evolutionary history of the Antarctic flora solely from contemporary species distributions. These questions require an approach combining a comprehensive knowledge of Antarctic plant species and their wider distribution throughout the world with studies into their genetic diversity and rates of evolution. In particular modern molecular methods can provide powerful insights into previous population fragmentation and bottlenecks, historical patterns of dispersal and gene flow, relatedness between Antarctic taxa, and also with those elsewhere. Such studies are at an early stage in Antarctica, although already generating exciting results – for example, the only molecular clock study published to date for any terrestrial organism in Antarctica (of the evolutionary relationships between endemic maritime and sub-Antarctic chironomid midges; Allegruci *et al.*, 2006) has proposed separation events on a similar timsescale (c. 40 million years) to that of the different tectonic elements now occupied by these species (Livermore *et al.*, 2005). Integration of all of these approaches will be critical in elucidating the biogeographic and evolutionary history of the Antarctic macroflora.

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Biosketches

Helen Peat runs the Data and Resource Centre of the British Antarctic Survey (BAS) Biological Sciences Division. This includes curation of the BAS herbarium and maintenance of a variety of long-term datasets including the Antarctic Plant Database. **Andrew Clarke** is an ecologist with over 30 years of experience in polar regions. His current research interests include the role of temperature in physiology and the influence of historical processes on global patterns of diversity. **Peter Convey** is a polar terrestrial ecologist, and has worked at the British Antarctic Survey since 1988. He has completed more than ten summer seasons in the Antarctic, and two on Arctic Svalbard. His research interests are wide ranging, including the evolution of life history strategies of Antarctic terrestrial biota, climate change and its biological consequences, and historical and contemporary Antarctic biogeography.

Editor: Pauline Ladiges

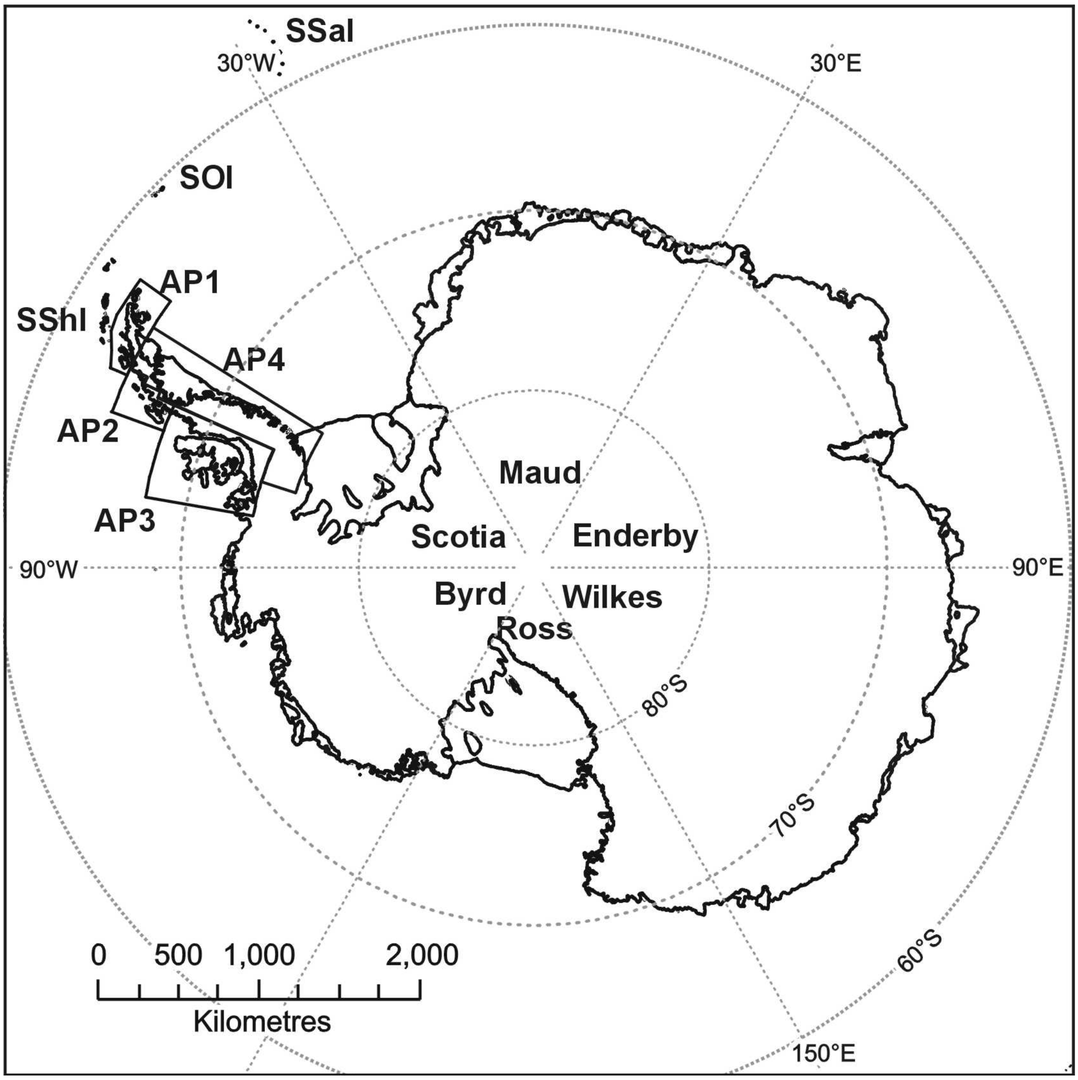


Fig. 1
A map of Antarctica showing the geographical regions into which distributional data were classified for biodiversity analyses. SSaI = South Sandwich Islands, SOI = South Orkney Islands, SShI = South Shetland Islands, AP = Antarctic Peninsula.

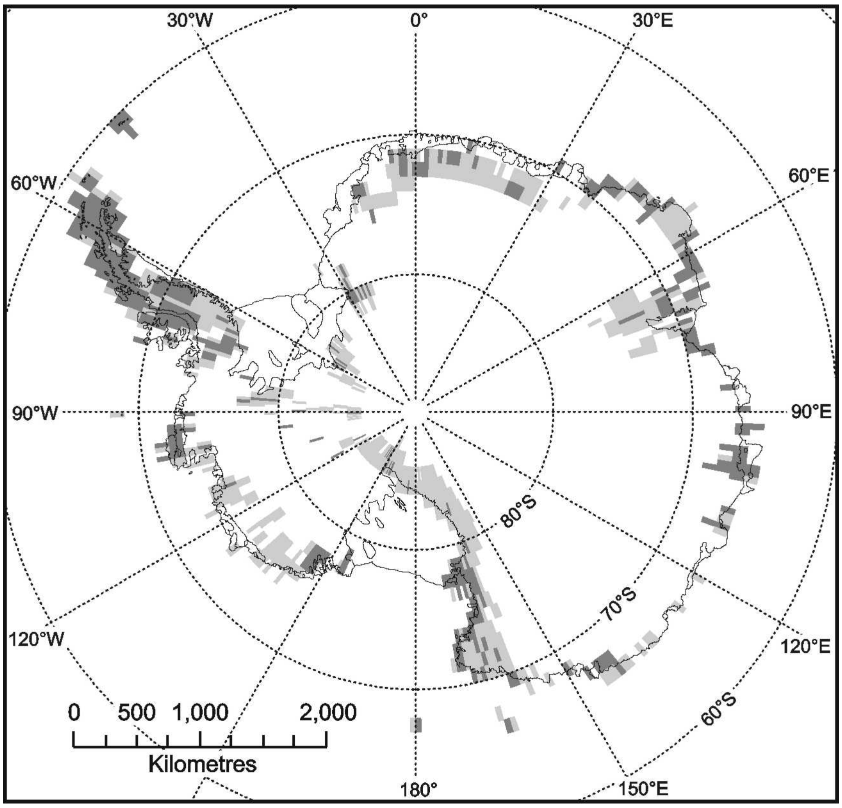


Fig. 2
A map of the Antarctic showing all one-degree latitude-longitude boxes containing ice-free ground. Boxes are shaded dark grey if plants have been recorded from within the box, and light grey if there are no plant records from within that box.

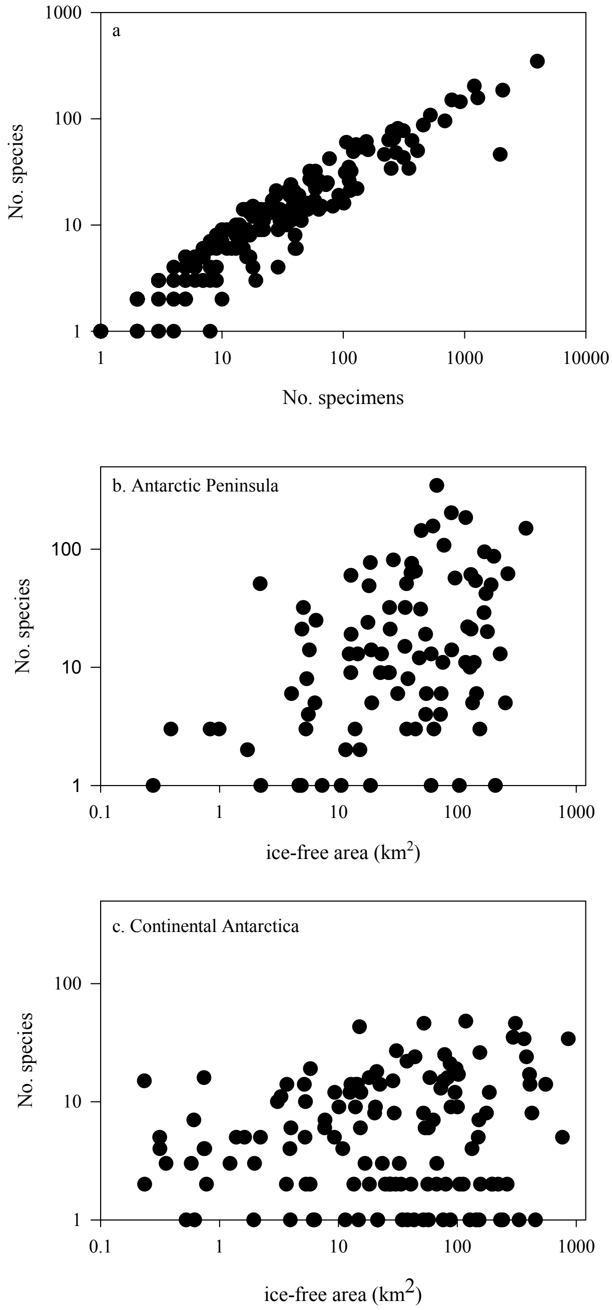


Fig. 3

a.) A plot of the number of specimens collected within each one degree box against the number of species recorded within that box. Only herbarium specimen data were used. Note that both axes are logarithmic.

b.) & c.) Plots showing the ice-free area and number of species recorded within each box of one degree latitude and longitude both on the Antarctic Peninsula and elsewhere on the Antarctic continent.

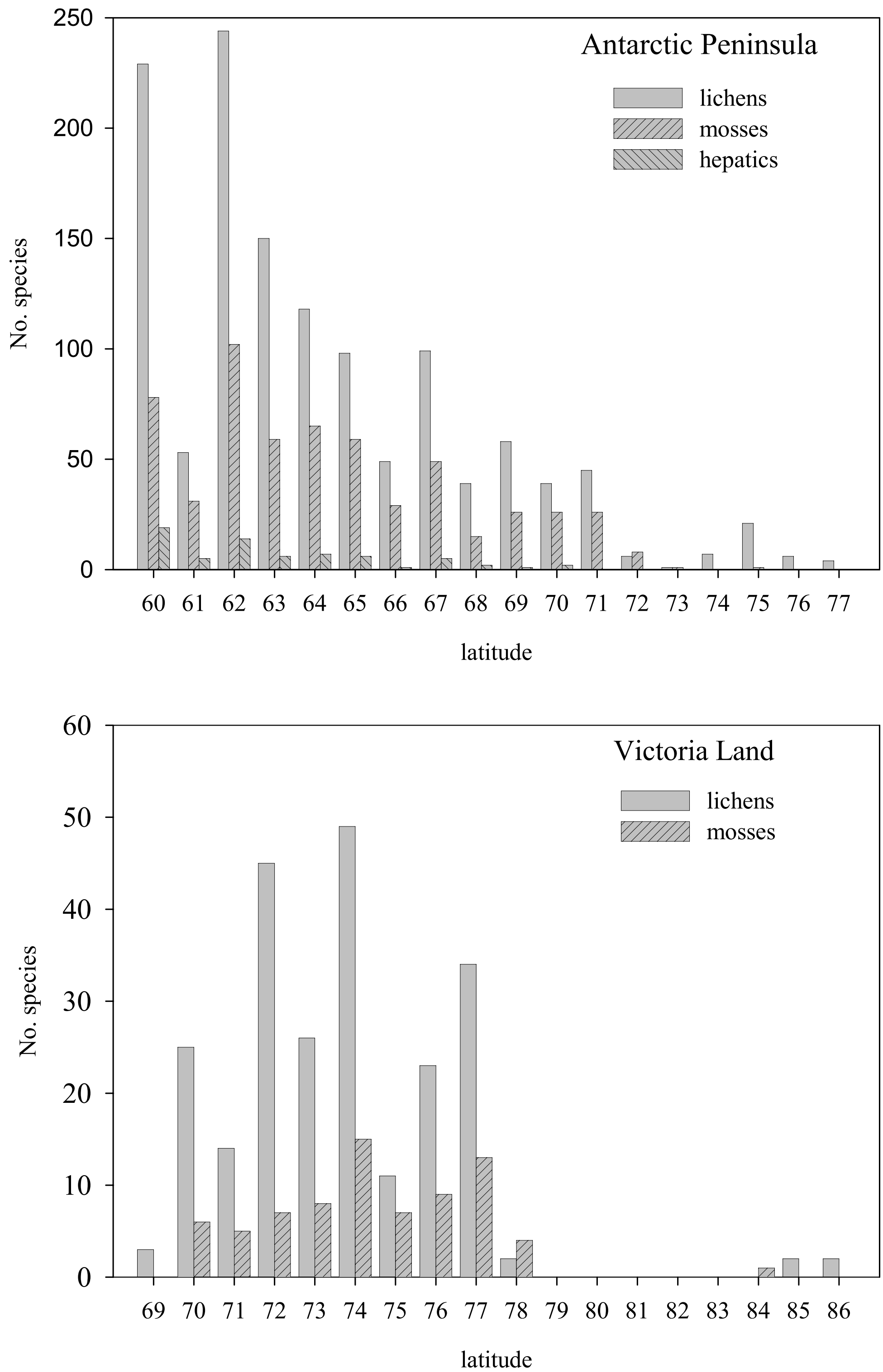


Fig. 4
The numbers of moss, lichen and hepatic species recorded from each degree of latitude along the Antarctic Peninsula (top) and in Victoria Land and the Transantarctic Mountains (bottom). No hepatics are shown in the latter region as only one species has been recorded from this area. Note the different scales on the y-axis.

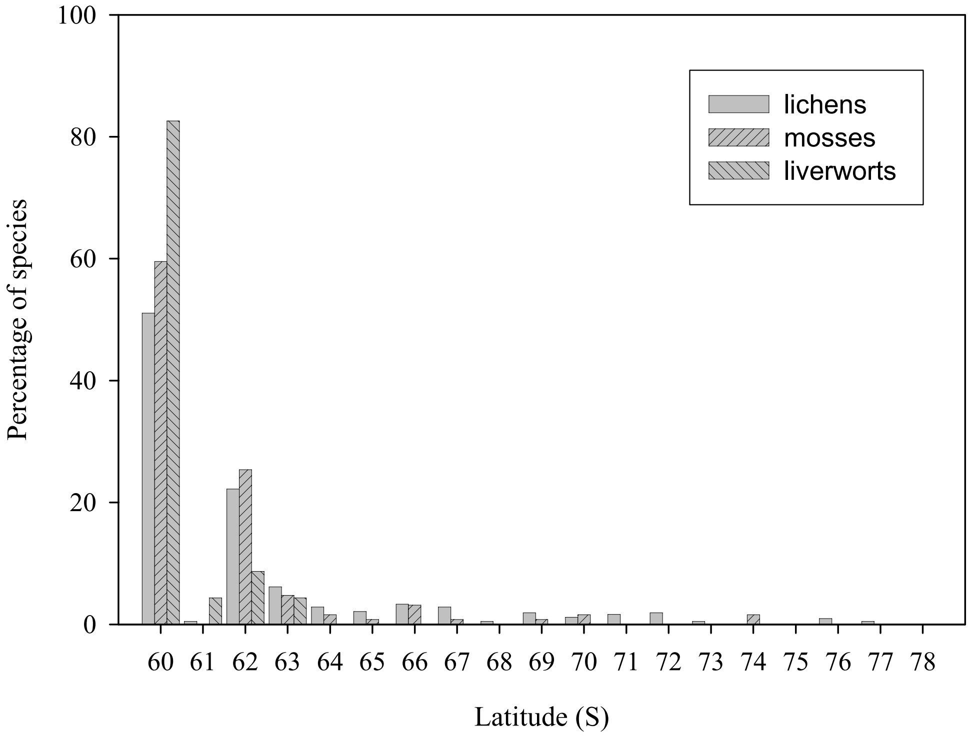
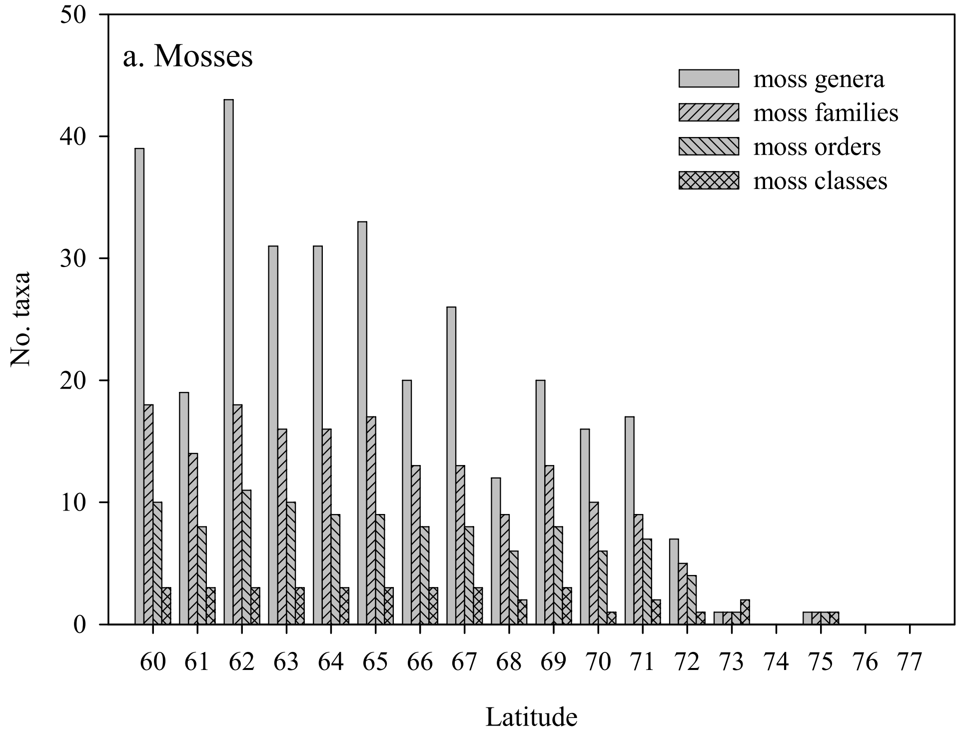
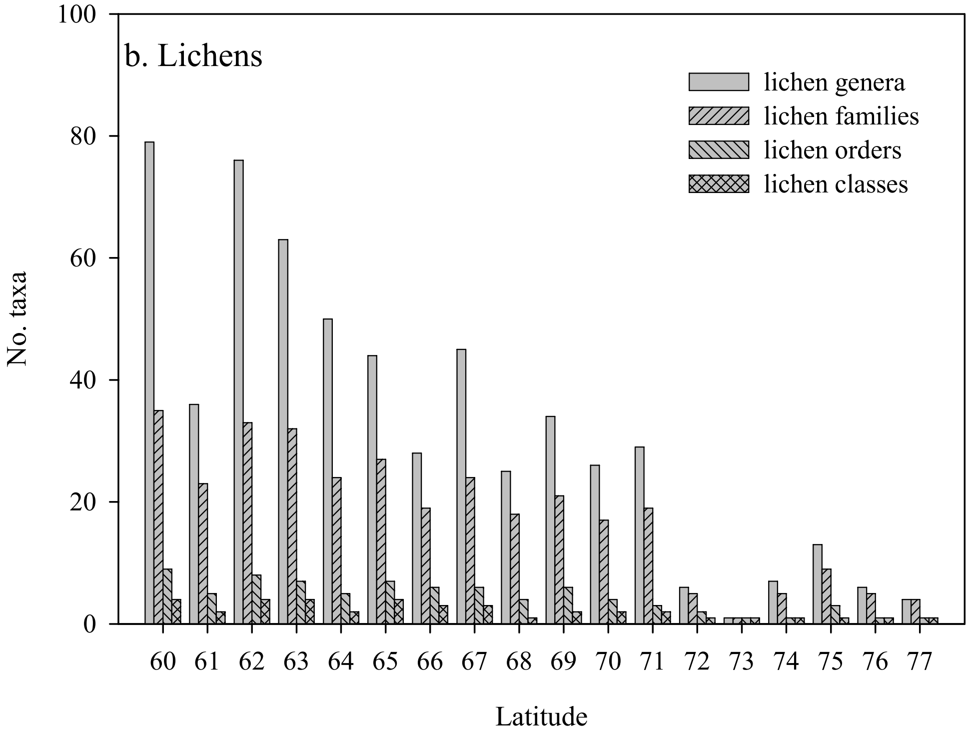
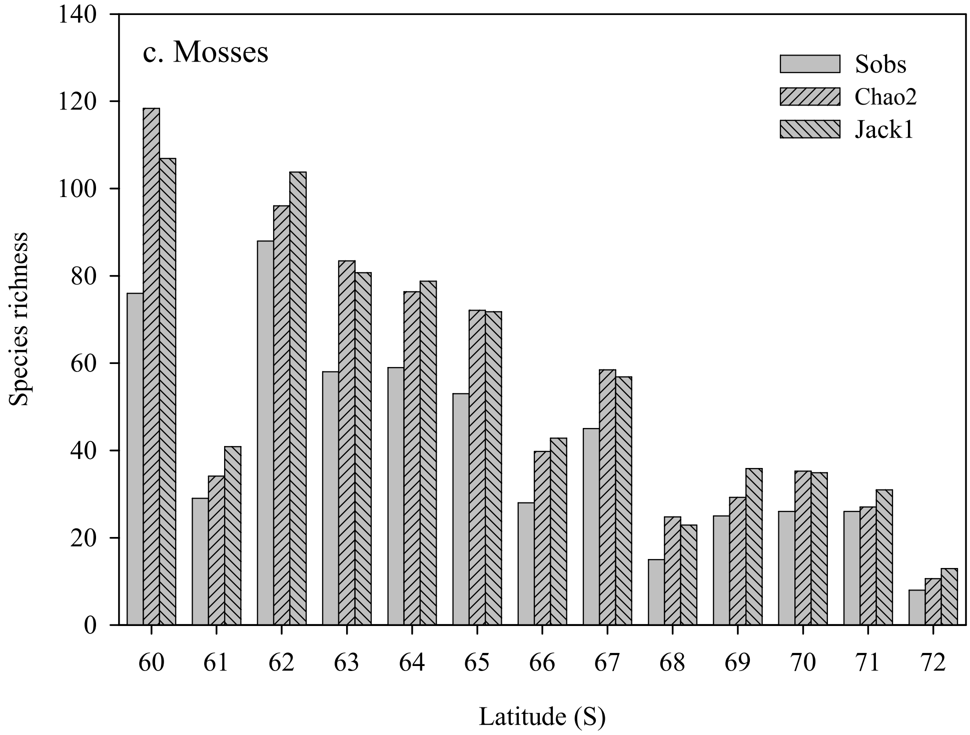


Fig. 5
Histogram showing the percentage of lichen, moss and liverwort species whose most northerly Antarctic Peninsula record occurs at each latitude band.


a. Mosses
moss genera
moss families
moss orders
moss classes
No. taxa
0
10
20
30
40
50
60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77
Latitude


b. Lichens
lichen genera
lichen families
lichen orders
lichen classes
No. taxa
0
20
40
60
80
100
60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77
Latitude



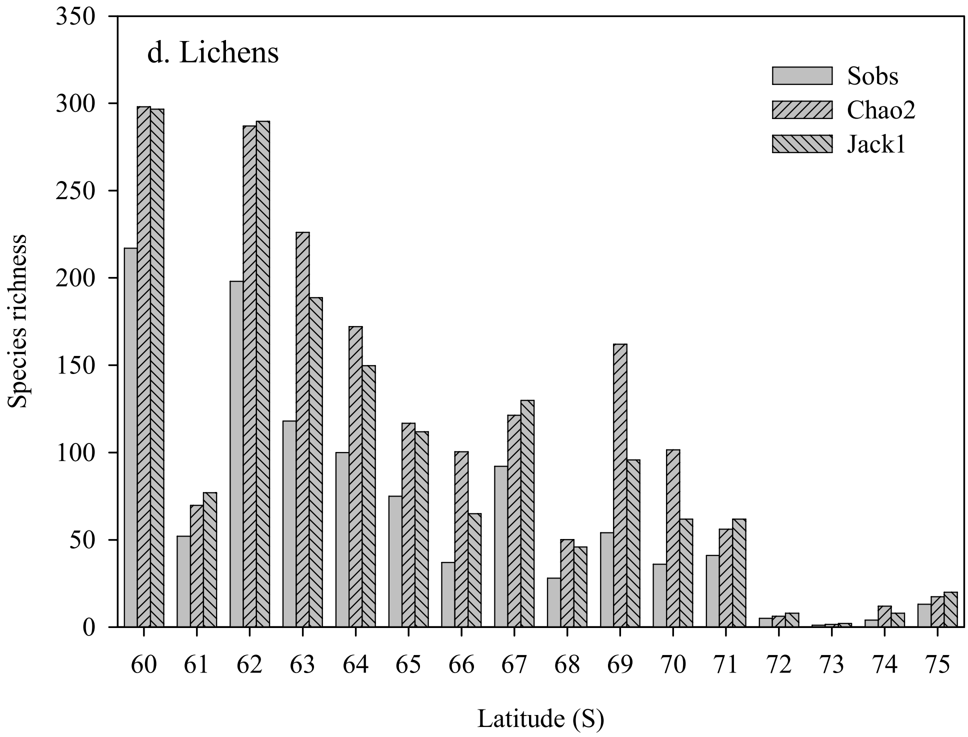


Fig. 6
a.) & b.) The number of moss (a) and lichen (b) genera, families, orders and classes within each latitude band on the Antarctic Peninsula.
c.) & d.) The number of observed species (based on herbarium specimens) within each latitude band on the Antarctic Peninsula and the estimated species richness using Chao2 and Jacknife1 estimators for mosses (c) and lichens (d).

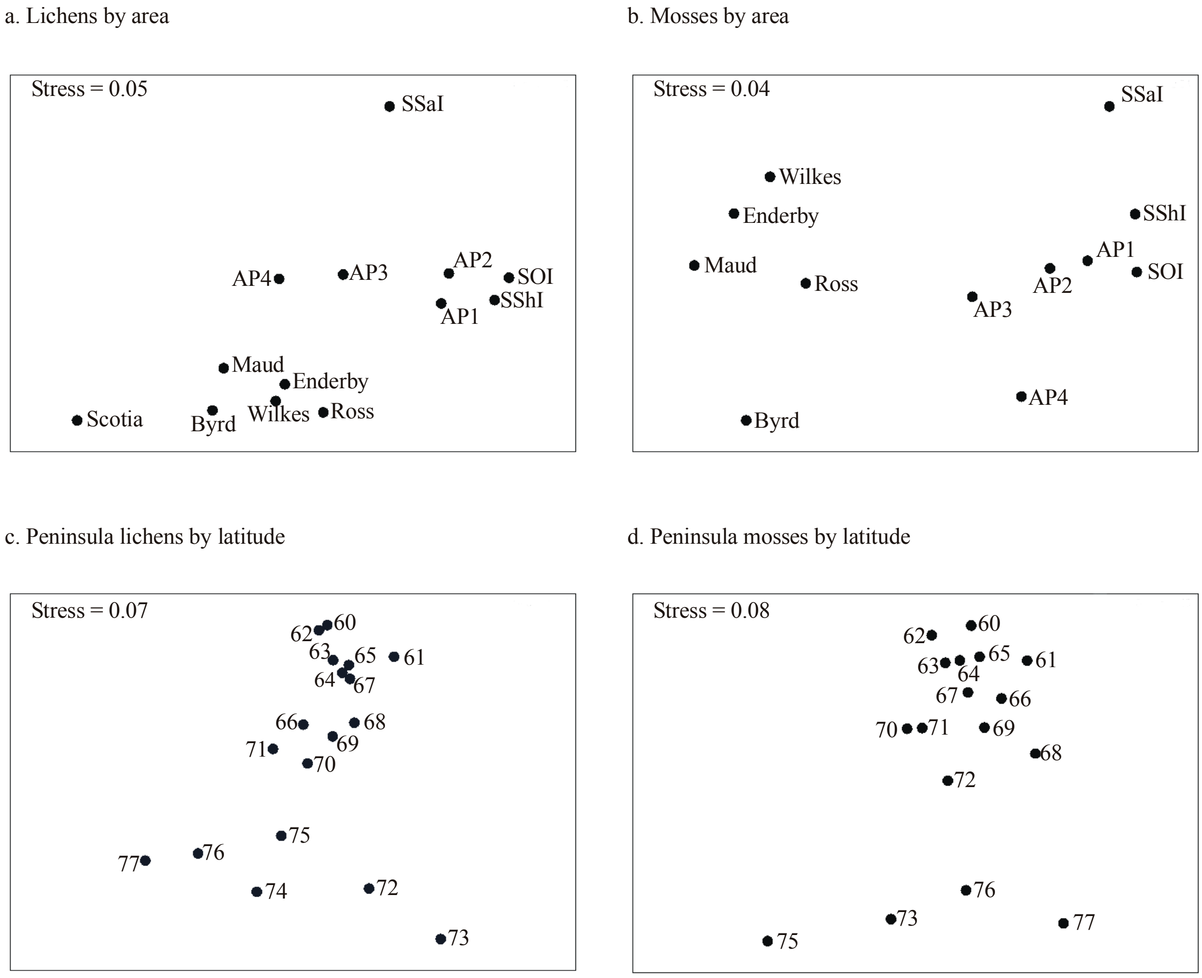
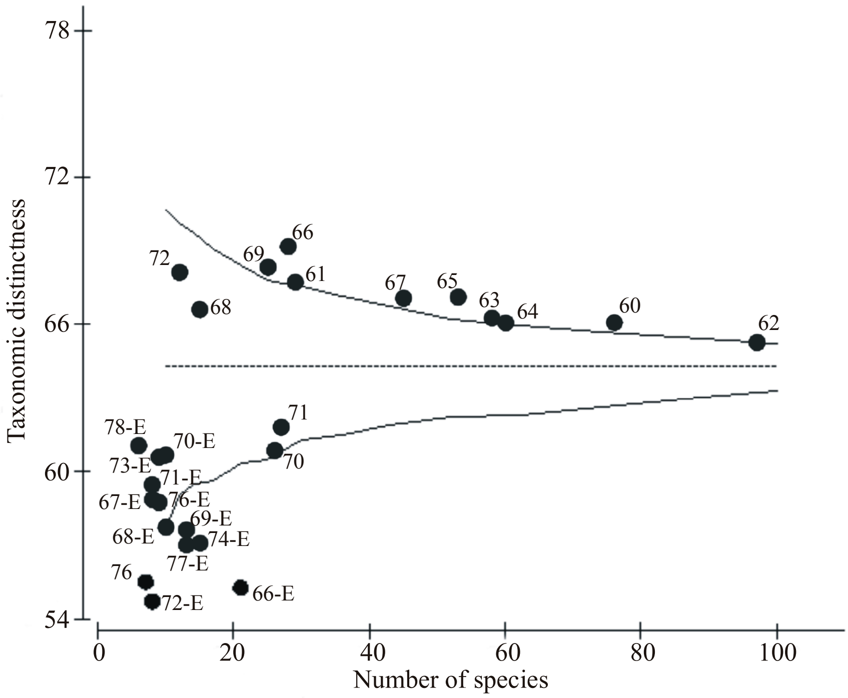


Fig. 7
MDS ordination of the similarity of different areas of Antarctica (a & b) and different latitudes on the Antarctic Peninsula (c & d) based on the presence and absence of lichen and moss species. Similarity has been measured using the Bray-Curtis resemblance measure. The stress level indicates how well the ordination represents the similarity values. Points close to each other are areas with similar species compositions and those further apart have more dissimilar species compositions. Scotia is absent in (b) as no mosses have been collected in non-Antarctic Peninsula parts of this region. SSaI = South Sandwich Islands, SOI = South Orkney Islands, SShI = South Shetland Islands, AP = Antarctic Peninsula.

a. Mosses



b. Lichens

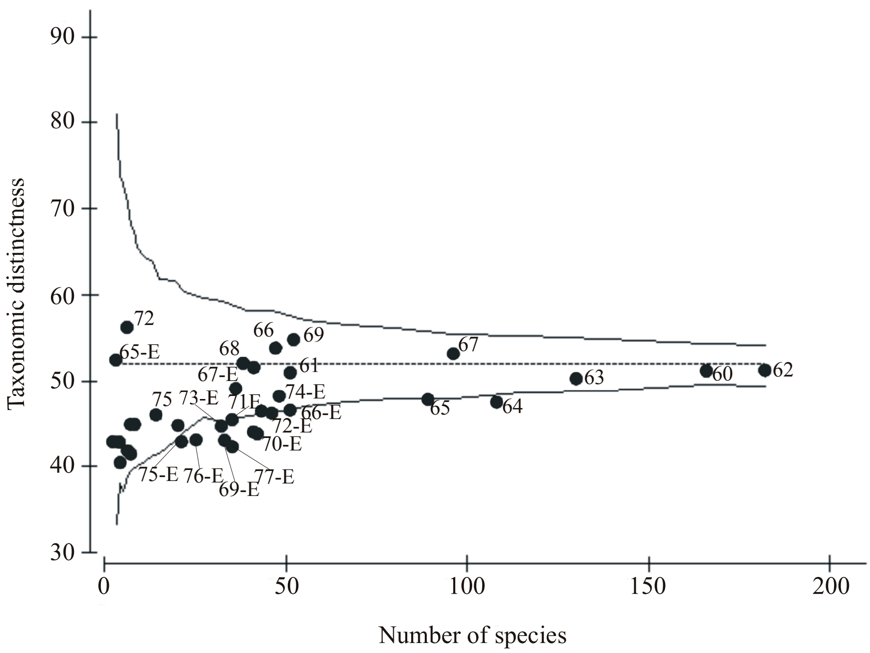


Fig. 8
Funnel plots for the taxonomic distinctness of Antarctic mosses and lichens. The solid lines show the area within which 95% of values fall and the dotted line the mean value when particular numbers of species are repeatedly selected at random from a pool of all Antarctic moss/lichen species. The points show the actual values for the species occurring at each degree of latitude with Peninsula occurrences separated from occurrences in East Antarctica (indicated by "E"). The labels on some non-significant points have been omitted for clarity.

Figure Legends

Fig. 1
A map of Antarctica showing the geographical regions into which distributional data were classified for biodiversity analyses. SSaI = South Sandwich Islands, SOI = South Orkney Islands, SShI = South Shetland Islands, AP = Antarctic Peninsula.

Fig. 2
A map of the Antarctic showing all one-degree latitude-longitude boxes containing ice-free ground. Boxes are shaded dark grey if plants have been recorded from within the box, and light grey if there are no plant records from within that box.

Fig. 3
a.) A plot of the number of specimens collected within each one degree box against the number of species recorded within that box. Only herbarium specimen data were used. Note that both axes are logarithmic.
b.) & c.) Plots showing the ice-free area and number of species recorded within each box of one degree latitude and longitude both on the Antarctic Peninsula and elsewhere on the Antarctic continent.

Fig. 4
The numbers of moss, lichen and hepatic species recorded from each degree of latitude along the Antarctic Peninsula (top) and in Victoria Land and the Transantarctic Mountains (bottom). No hepatics are shown in the latter region as only one species has been recorded from this area. Note the different scales on the y-axis.

Fig. 5
Histogram showing the percentage of lichen, moss and liverwort species whose most northerly Antarctic Peninsula record occurs at each latitude band.

Fig. 6
a.) & b.) The number of moss (a) and lichen (b) genera, families, orders and classes within each latitude band on the Antarctic Peninsula.
c.) & d.) The number of observed species (based on herbarium specimens) within each latitude band on the Antarctic Peninsula and the estimated species richness using Chao2 and Jacknife1 estimators for mosses (c) and lichens (d).

Fig. 7
MDS ordination of the similarity of different areas of Antarctica (a & b) and different latitudes on the Antarctic Peninsula (c & d) based on the presence and absence of lichen and moss species. Similarity has been measured using the Bray-Curtis resemblance measure. The stress level indicates how well the ordination represents the similarity values. Points close to each other are areas with similar species compositions and those further apart have more dissimilar species compositions. Scotia is absent in (b) as no mosses have been collected in non-Antarctic Peninsula parts of this region. SSaI = South Sandwich Islands, SOI = South Orkney Islands, SShI = South Shetland Islands, AP = Antarctic Peninsula.

Fig. 8
Funnel plots for the taxonomic distinctness of Antarctic mosses and lichens. The solid lines show the area within which 95% of values fall and the dotted line the mean value when particular numbers of species are repeatedly selected at random from a pool of all Antarctic

moss/lichen species. The points show the actual values for the species occurring at each degree of latitude with Peninsula occurrences separated from occurrences in East Antarctica (indicated by “E”). The labels on some non-significant points have been omitted for clarity.

Table 1
The number of specimen and literature records for different areas in the Antarctic (see Fig. 1), the area of available land in each area (ignoring sea and ice shelf) and the percentage of that area which is not permanently covered in ice

Area	Number of herbarium specimens	Number of literature records	Area of land in sector (km^2)	% ice free area
South Sandwich Islands	1262	0	?	?
South Orkney Islands	6385	4	626	15.80
South Shetland Islands	7272	1002	3825	11.00
Antarctic Peninsula (60-65°S)	4805	156	26424	6.50
Antarctic Peninsula (65-70°S)	5925	62	89728	2.30
Scotia Sector south of 70°S	2238	6	1052404	0.60
Byrd sector	706	4	1468872	0.15
Ross Sector	3159	238	877184	2.40
Wilkes Sector	3255	333	3422403	0.02
Enderby Sector	1159	704	3001835	0.24
Maud Sector	366	219	2026965	0.18

Table 2

Proposed division of Antartica into phytogeographic zones, with number of species recorded from each. Zones modified from Lewis Smith (1984), Bednarek-Ochyra *et al*. (2000)

Region	Province	Description	Localities	Diversity
Maritime Antarctic	Northern	Cold moist maritime climate. Semi-desert dominated by cryptogams but including small closed stands of the only two phanerogams in the Antarctic	South Sandwich Islands?, South Orkney Islands, South Shetland Islands, west coast of Antarctic Peninsula and offshore islands to c. 68°S. North east coast of Peninsula to 65°S.	Mosses 100-115 Lichens c. 350 Liverworts 27 Phanerogams 2
	Southern	Cold dry maritime climate. Semi-desert dominated by cryptogams but with lower diversity than northern province	West coast of Antarctic Peninsula and offshore islands from 68°S to c. 72°S. East coast of Antarctic Peninsula from 65°S.	Mosses 40-50 Lichens c. 120 Liverworts 2 Phanerogams 2
Continental Antarctica	Coastal & Slope (provinces not distinguished in this study)	Cold arid climate. Semi-desert or desert with restricted moss vegetation and numerous lichens locally forming extensive stands	Eastern Antarctica and western Antarctica south of 72°S.	Mosses 20-30 Lichens c. 90 Liverworts 1 Phanerogams 0