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Conservation biogeography of the Antarctic

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ABSTRACT

Aim To present a synthesis of past biogeographic analyses and a new approach based on spatially explicit biodiversity information for the Antarctic region to identify biologically distinct areas in need of representation in a protected area network.

Location Antarctica and the sub-Antarctic.

Methods We reviewed and summarized published biogeographic studies of the Antarctic. We then developed a biogeographic classification for terrestrial conservation planning in Antarctica by combining the most comprehensive source of Antarctic biodiversity data available with three spatial frameworks: (1) a 200-km grid, (2) a set of areas based on physical parameters known as the environmental domains of Antarctica and (3) expert-defined bioregions. We used these frameworks, or combinations thereof, together with multivariate techniques to identify biologically distinct areas.

Results Early studies of continental Antarctica typically described broad bioregions, with the Antarctic Peninsula usually identified as biologically distinct from continental Antarctica; later studies suggested a more complex biogeography. Increasing complexity also characterizes the sub-Antarctic and marine realms, with differences among studies often attributable to the focal taxa. Using the most comprehensive terrestrial data available and by combining the groups formed by the environmental domains and expert-defined bioregions, we were able to identify 15 biologically distinct, ice-free, Antarctic Conservation Biogeographic Regions (ACBRs), encompassing the continent and close lying islands.

Main conclusions Ice-free terrestrial Antarctica comprises several distinct bioregions that are not fully represented in the current Antarctic Specially Protected Area network. Biosecurity measures between these ACBRs should also be developed to prevent biotic homogenization in the region.

Keywords
Antarctic biodiversity, biogeographical zones, conservation planning, ice-free Antarctica, spatial ecology, sub-Antarctic biogeography.

INTRODUCTION

Antarctica and the Southern Ocean are often considered among the world's last great wildernesses. Although past whaling and sealing have substantially altered the Southern Ocean ecosystem (Trathan & Agnew, 2010), both terrestrial and marine areas have a relatively small human footprint in comparison with many other regions globally (Sanderson *et al.*, 2002). Moreover, the Antarctic continent and the Southern Ocean south of 60°S enjoy substantial protection under the Antarctic Treaty System (Berkman *et al.*, 2011). Nonetheless, concern about the conservation of the Antarctic is mounting (Hughes & Convey, 2010). Predominant among the pressures on its biodiversity include growing

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exploitation of marine systems, biological invasions, ocean acidification, localized pollution, and the effects of climate change (Tin *et al.*, 2009; Aronson *et al.*, 2011; Trivelpiece *et al.*, 2011).

In terrestrial systems, the most significant threats are the impacts of climate change, invasive species, and their interaction (Walther *et al.*, 2002; Frenot *et al.*, 2005). Growing science and tourist activities across the region coupled with climate change are of particular concern. Not only are they likely to exacerbate the impacts of non-indigenous species that are already present (Kennedy, 1995; Bergstrom & Chown, 1999; Chown *et al.*, 2007), but they are also increasing the probability of the introduction of additional species from outside the region (Whinam *et al.*, 2005; Lee & Chown, 2009; Chown *et al.*, 2012) and the likelihood of intra-regional propagule movements that can lead to biological homogenization (Hughes & Convey, 2010). Indeed, such impacts and events have already been documented (Frenot *et al.*, 2005; Shaw *et al.*, 2010; Lebouvier *et al.*, 2011; Lee & Chown, 2011; Olech & Chwedorzewska, 2011), and much concern has been expressed that the conservation value of the terrestrial Antarctic and its surrounding islands is being compromised (Rogan-Finnemore, 2008), as are the signals of the biological history of the continent (Cowan *et al.*, 2011; Hughes & Convey, 2012). In the latter case, molecular studies are demonstrating that the biogeography of the continent and its surrounding islands is more complicated than originally thought (Stevens *et al.*, 2006; Chown & Convey, 2007; Convey *et al.*, 2008; De Wever *et al.*, 2009; Mortimer *et al.*, 2011), with substantial landscape genetic complexity even over relatively limited spatial extents (Stevens & Hogg, 2006; Van de Wouw *et al.*, 2007; McGaughran *et al.*, 2010). At the same time, the scope and speed of human travel across the entire continent is growing as air networks are developed across increasingly large parts of it, so increasing the potential for homogenization (Hughes & Convey, 2010). Most of this increasing human presence and associated infrastructure is focused on ice-free areas of the terrestrial environment (Hull & Bergstrom, 2006).

As with any area subject to multiple use (here science and tourism), conservation management of the terrestrial Antarctic requires information that can be used to reduce likely threats to biodiversity, and the historical signals it represents, to a minimum given the other uses. Conservation management planning typically commences with some form of classification system to identify an enduring set of sites that are representative of the biodiversity features of a region (Margules & Pressey, 2000). How this might be achieved, which schemes should be used, and how other activities, land uses or values should be included in any optimization approach have been much discussed (e.g. Rondinini *et al.*, 2006; Seo *et al.*, 2009; Wilson *et al.*, 2010; Carvalho *et al.*, 2011), but understanding the distribution of diversity at one or more spatial scales forms the core of all of these approaches, which are in essence concerned with conservation biogeography (Whittaker *et al.*, 2005). Clearly, both insufficient spatially explicit distribution information and taxonomic knowledge (i.e. the Wallacean and Linnean shortfalls, see Whittaker *et al.*, 2005) will substantially influence any attempt at understanding the spatial distribution of diversity. However, because the consequences of conservation inaction can be substantial, such understanding often must be developed with the tools and data at hand (Soulé, 1991; Hughes & Convey, 2012).

Despite a long history of biogeographic research in the Antarctic, spatially explicit conservation planning frameworks for the region are largely lacking. An early effort suggested how this might be done (Usher & Edwards, 1986). The concept was not developed further with the exception of one study across the Southern Ocean Islands, which sought to explore the network of islands that would represent most indigenous species while capturing fewest introduced ones (Chown *et al.*, 2001). To some extent, the situation could be ascribed to a lack of spatially explicit data for most taxonomic groups on the continent (e.g. Peat *et al.*, 2007; Hughes & Convey, 2012). However, alternative approaches, such as those using other environmental features, including better known taxa or abiotic variables (for discussion see e.g. Sarkar *et al.*, 2006; Rodrigues & Brooks, 2007; Jackson & Gaston, 2008; Lewandowski *et al.*, 2010), have also typically not been adopted.

One exception is an Environmental Domains of Antarctica (EDA) analysis based on abiotic variables (Morgan *et al.*, 2007) that was adopted at the 31st Antarctic Treaty Consultative Meeting (ATCM). The meeting recommended that the EDA be used in conjunction with other tools agreed within the Antarctic Treaty System as a dynamic model for the identification of areas that could be designated as Antarctic Specially Protected Areas within the '*systematic environmental-geographical framework*' explicitly called for in Annex V of the Protocol on Environmental Protection to the Antarctic Treaty (http://www.ats.aq/e/ats.htm). The Protocol lays out the framework for conservation of the region through the Antarctic Treaty System. However, the EDA contains no biological information. Our aim here is therefore to develop further the EDA with additional data on the distribution of biodiversity to provide a systematic environmental-geographical framework comprised of a first tier, spatially explicit set of Antarctic Conservation Biogeographic Regions.

In doing so, we adopt an explicitly historical view, acknowledging previous biogeographic work. Thus, we provide a brief historical overview of the available biogeographic classifications that have been adopted for the continent and, in the language of the Antarctic Treaty (see http://www.ats.aq/e/ats.htm), its associated and dependent systems (the Southern Ocean and the sub-Antarctic islands specifically, although we include most of the Southern Ocean Islands – see Chown *et al.*, 1998 for rationale). Doing so provides the basis for understanding previous attempts at bioregionalization of the Antarctic continent and its surrounding ocean and islands, and their implications for a modern conservation biogeography of the region. Next, we describe a set of physical environmental domains for the continental Antarctic that were developed using abiotic variables (i.e. the EDA), which provide surrogate features for spatial conservation of biodiversity. We then describe an additional set of bioregions that were identified using a nominal group method of expert consultation (*sensu* Sutherland, 2006). We examine the relationships between these classifications using spatially explicit biodiversity data currently available through the Scientific Committee for Antarctic Research (SCAR) Antarctic Biodiversity Database (ABD) (http://data.aad.gov.au/aadc/biodiversity/) Finally, we identify a set of areas that, given current spatial and taxonomic resolutions, represent a minimal set that should be fully represented in a terrestrial Antarctic protected area system to capture the continent's biodiversity, and between which propagule transfer should be reduced to a minimum. In the case of the sub-Antarctic islands, we draw on previous analyses that have largely provided similar information (e.g. Chown *et al.*, 2001; Greve *et al.*, 2005; Shaw *et al.*, 2010).

METHODS

Historical review

The historical review was based on a search conducted using ISI Web of Science using the terms 'Antarctic*', 'sub-Antarctic*', 'subantarctic*', the names of the islands in the region and the term 'biogeog*'. In addition, various key older works identified within the papers sourced using the first approach were consulted (e.g. Carrick *et al.*, 1964; Holdgate, 1970; Laws, 1984; Pickard & Seppelt, 1984; Longton, 1988). The classification schemes and approaches used were then sourced from the original works. Where the scheme was based on the author's knowledge and views based on the distribution of species, we described this as 'geographical distribution', whereas if a particular analytical approach was adopted, we described these using either the author's terms or using a modern equivalent.

For the more modern analyses (typically post-1995, but see also Pickard & Seppelt, 1984), formal techniques were more often used in the biogeographic assessments and usually involved some form of cluster analysis (e.g. McInnes & Pugh, 1998; Barnes & Griffiths, 2008). In these cases, we indicate the major classifications and methods used. These techniques do not lend themselves to meta-analysis. While a supermatrix approach (see e.g. Smith *et al.*, 2009) could have been adopted, we elected not to do so because any supermatrix approach might be dominated by the most abundant taxon and would not reflect biological differences (such as in dispersal ability) among taxa (Greve *et al.*, 2005). While much debate exists about the validity of various biogeographic classification approaches (see Morrone & Crisci, 1995; Brooks & Van Veller, 2003; Morrone, 2005; Ronquist & Sanmartin, 2011 for further discussion), we elected simply to recognize that these methods have various strengths and weaknesses.

Current biodiversity data

For the assessment of current continental diversity patterns, we accessed data from the ABD, a SCAR initiative that currently contains over 100 collections of data and more than 500,000 records (http://data.aad.gov.au/aadc/biodiversity/).

While both the historical and more modern work has focussed on all aspects of the biogeography of the region, for the quantitative analyses, we maintained a strict focus on ice-free areas of the Antarctic continent and Antarctic Peninsula islands (not including South Sandwich Islands) because these have been least represented in recent, spatially explicit work at anything but the coarsest, geopolitical scale. Moreover, the Southern Ocean Islands have been comparatively well studied (see Introduction), and marine areas are currently the focus of a large bioregionalization approach based on data collected as part of the Census of Antarctic Marine Life (see Griffiths, 2010; Rice *et al.*, 2011). In consequence, marine and sub-Antarctic ABD records were first excluded from the data obtained for the analyses. The remaining terrestrial Antarctic records were checked for spatially explicit data and taxonomic reliability. Twelve collections were identified as containing useful data, and each was converted to a separate spatial layer using Manifold® Professional v8.0 GIS software (Manifold Software Ltd). Collections were then assessed on the type and accuracy of the spatial data associated with them, the number of records, how the data were collected and the number and type of taxa (and taxonomic resolution).

In some cases, where inconsistencies or anomalies were identified, the raw collection data were consulted and corrections were carried out. These included spatial corrections using published sources (including the SCAR Composite Gazetteer http://data.aad.gov.au/aadc/gaz/scar/) or the authors' knowledge. The taxonomic resolution of each record was also checked; subspecies or infraspecies were removed, as were those records with any taxonomic uncertainty. This left a total of 38,854 records and 1823 taxa remaining in the 12 collections, and these formed the basis of our analyses. Records covered the entire Antarctic continent and included a diverse range of terrestrial taxa with over 30 phyla represented (see Table S1 in Supporting Information). Some of the data used here (e.g. plant data from British Antarctic Survey and the Australian Antarctic Division Herbarium) have been described elsewhere (e.g. Peat *et al.*, 2007).

Quantitative approaches

As a first-level assessment of the biodiversity data, we created a grid of 200 × 200 km squares overlaid on Antarctica (generating 406 cells), constrained by the extent of ice-free areas (142 cells) obtained from the most up-to-date map of ice-free areas of Antarctica (provided by the Australian Antarctic Data Centre from the Antarctic Digital Database V5© Scientific Committee for Antarctic Research 1993–2006). A cell size of 200 × 200 km was used to maintain a constant area across the continent, and as a compromise between point data and cells that would encompass multiple regions, making analysis less meaningful. Species records were then attributed to each cell and the numbers of records and numbers of species for each cell summed. Pilot analyses (see Appendix S1 in Supporting Information) indicated substantial variation in the number of records and number of species per 200 km cell, with strong relationships between them, and approximately 1/3 of cells containing no records (see Figs S1, S2 in Supporting Information). In consequence, we elected not to attempt analysis of relationships among areas (see Fig. S3 in Supporting Information) using data at this resolution. In our exploratory analyses, the physical data used in the environmental domains analyses were also interpolated to the 200-km grid spatial framework. Generalized dissimilarity modelling (Ferrier *et al.*, 2007; R Development Core Team, 2010) was then used to examine the relationship between the underlying physical attributes of the environment and the observed patters of biodiversity (see Appendix S2 in Supporting Information). As might be expected from our initial analyses, little additional resolution was achieved, confirming our decision not to work at the 200-km resolution (see Fig. S4 in Supporting Information).

Environmental domains

Recently, a set of environmental domains for Antarctica were developed based purely on abiotic environmental data (Morgan *et al.*, 2007). The classification of the environmental domains used spatially explicit numerical data layers that describe aspects of Antarctica's climate, ice cover and geology (for detailed methodology and data layer source information see Appendix S3 in the Supporting Information). The approach was based on the process used to capture the environmental domains for New Zealand (Leathwick *et al.*, 2003). This two-stage classification process begins with a non-hierarchical classification that groups similar points together based on a range of abiotic environmental data. A hierarchical classification was used to define inter-environment relationships between centroids for each of the environments identified by the non-hierarchical classification. The results of these classifications were then projected back into a spatially explicit data layer using ARCVIEW v9.1 GIS software (Environmental Systems Research Institute). Following this non-hierarchical classification, which resulted in approximately 400 environmental domains being created, the groups were agglomerated down to 21 distinct environments using expert consultation. Nine of these environmental domains encompass ice-free areas (Fig. 1).

Expert-defined bioregions

We used expert consultation to provide a consensus view of biogeographic regions (bioregions) of the Antarctic (reflecting the experts' own work and previous biogeographic classifications). These bioregions were obtained by a nominal group method of expert consultation (Sutherland, 2006). In essence, we began with a Delphi analysis in which five recognized experts (see Appendix S4 in Supporting Information) were independently requested to define regions in Antarctica they believed to be distinct in terms of their biodiversity. Polygons of bioregions were then created using ARCVIEW v9.1 GIS software (ESRI) on a base map of the region. These maps were examined by a larger group of experts ($n = 10$ see Appendix S4) and modified following discussion to provide a final set of bioregions (Fig. 2).

Analyses

We allocated records from the biodiversity database to each of the domains, or bioregions, respectively, using Manifold® Professional v8.0 GIS software (Manifold Software Limited), and examined the relationships between the environmental domains or bioregions. To do so, each of the presence–absence matrices was used to construct a Jaccard similarity matrix, which was in turn used to undertake group-average cluster analysis (using Primer v6 – Primer-E, Plymouth, UK). To ascertain the level of structure present in the groups formed by each dendrogram, a similarity profile routine (SIMPROF – Primer v6, see Clarke *et al.*, 2008) was run with 10,000 simulations and the stopping rule specified at the 5% significance level. SIMPROF is a permutation-based procedure that ranks the pairwise similarities in each group and tests the null hypothesis that samples were all drawn from the same species assemblage.

The SIMPROF groups formed by the two dendrograms were compared explicitly to find areas that matched, or more specifically, where a domain group (or geographically distinct subset thereof) was encapsulated by a bioregion group. In a few cases there was a one-to-one match between a single domain group and a single bioregion group. These areas were considered biologically distinct and termed Antarctic Conservation Biogeographic Regions (ACBRs) here. Where a one-to-one match did not occur, groups formed by the bioregion cluster analyses (designated by the B prefix) were used to partition off geographically distinct subsets of the domain groups (designated by the D prefix). The key principle adopted was the identification of geographically distinct subsets of the domain groups, and the containment of them within bioregion groups. Specific details of the comparisons, matches and subsets of the two cluster analyses are provided in Appendix S5.

RESULTS

Prior biogeographic classifications

The Antarctic region has traditionally been described as the southern limit of the high forest (Godley, 1960; Skottsberg, 1960), and divided into four main regions: Southern Cold Temperate, Sub-Antarctic, Maritime Antarctic, and Conti-

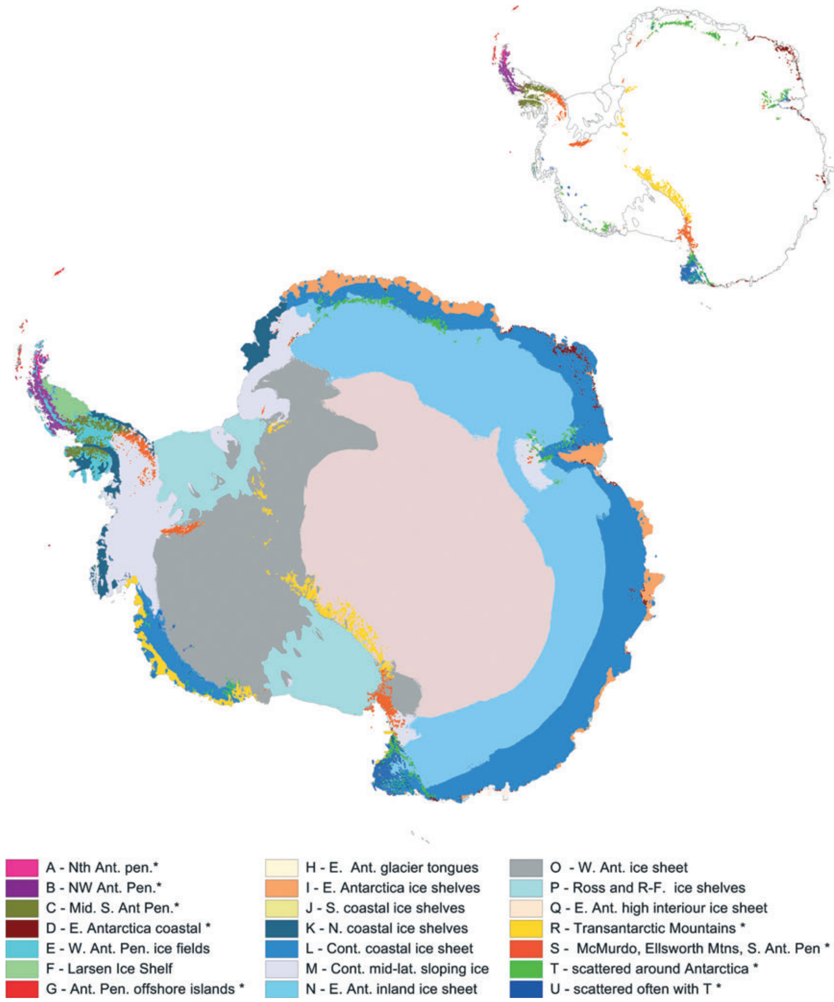

Figure 1 Environmental Domains of Antarctica. Inset shows environmental domains that enclose ice-free areas, denoted by * in legend. Raster data layers and shapefiles available on request from Landcare Research New Zealand at http://www.landcareresearch.co.nz/research/soil/Ant_soils/eda.asp. Detailed maps of each domain in technical report available at http://www.ats.aq/devEM/documents/001718_np.pdf.

nental Antarctic (Table 1). This scheme has predominated in a wide range of works based on explicit (see Table S2 in Supporting Information) or implicit (see Table S3 in Supporting Information) biogeographic analyses, although with a tendency to increase the number of sub-divisions among regions especially as more quantitative methods have been applied. For example, earlier studies tended to define the maritime Antarctic as primarily the west coast of the Antarctic Peninsula, where cryptogamic development is significant (e.g. Holdgate, 1970) while later studies have argued that revision of this biogeography is required (see the Gressitt Line of Chown & Convey, 2007). Nevertheless, several studies have recognized the shortcomings of such a simplistic classification scheme and have either shown or suggested that bioregionalization of Antarctic is more complex (e.g. Weyant, 1966; Pickard & Seppelt, 1984; Smith, 1984; Peat *et al.*, 2007; Pugh & Convey, 2008). One exception to this general approach is the one first described by Greene *et al.* (1970) and extended by Pugh (1993), where Antarctica is divided into 8–11 largely arbitrary regions based on traditionally recognized geographic locations and to a lesser extent on geopolitical boundaries. A similar set of broad geographic zones were proposed by Keage (1987); however, he delineated areas on the basis of different ice-catchment areas and glaciological boundaries. By complete contrast, modern genetic studies have described considerable biogeographic complexity (Allegrucci *et al.*, 2006; Stevens & Hogg, 2006; De Wever *et al.*, 2009; McGaughran *et al.*, 2010; Wagstaff *et al.*, 2011), although at present too few studies have been undertaken to apply formal phylogenetic methods to construct a phylogeography of the continent.

Classification of the sub-Antarctic region (and indeed the Southern Ocean Islands as a whole) has been more contentious, with opinions ranging from a single unit – Insulantarctica, to what is essentially either a set of ocean province regions (Atlantic, Pacific and Indian) (e.g. Smith, 1984), or regions

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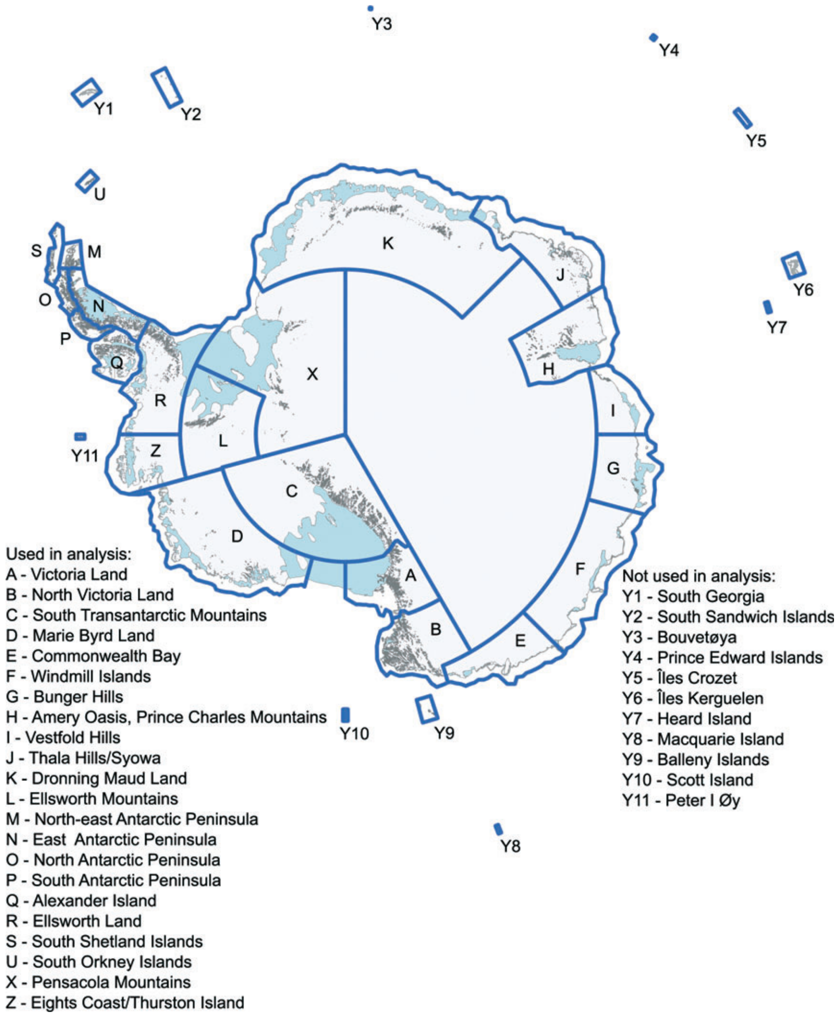

Figure 2 Expert-defined bioregions of Antarctica. The Southern Ocean Island bioregions (prefixed with Y) were not used in the analysis but are included here for completeness. Shapefile available from the Australian Antarctic Data Centre http://data.aad.gov.au/aadc/biodiversity. Ice-free regions are shown in dark grey (ice-free layer provided by the Australian Antarctic Division Data Centre from the Antarctic Digital Database V5© SCAR 1993–2006).

Table 1 Classic zonation classification scheme with definitions and regions (Holdgate, 1970)

Zone	Botanical definition	Region covered
Southern cold temperate	From the Subtropical Convergence southward to the southern limit of dwarf shrub vegetation	Falkland Islands, Tristan da Cunha, St Paul, Amsterdam Island, New Zealand shelf islands
Sub-Antarctic	From the southern limits of dwarf shrub vegetation to the southern limit of extensive, closed phanerogamic vegetation	South Georgia, Prince Edward Islands, Îles Crozet, Îles Kerguelen, Heard Island, Macquarie Island
Maritime (or oceanic) Antarctic	From the southern limit of extensive, closed phanerogamic vegetation to the southern limit of extensive and relatively rich closed cryptogamic (especially bryophyte) communities.	South Sandwich, South Orkney, South Shetland Islands, Palmer Archipelago, west coast of Antarctic Peninsula south to Marguerite Bay, Bouvetøya, Peter 1 Øy
Continental Antarctic	South from the southern limit of extensive diverse closed cryptogram communities	The main continental mass of Antarctica

that are associated with given continental areas (Neotropical, Afrotropical and Australasian) (Gressitt, 1970; Morrone, 1998), irrespective of the analytical approach adopted (see Table S4 in Supporting Information). The diversity of classifications to some extent reflects the taxa used in a given study (Greve *et al.*, 2005) and the level at which given authors elect to define regions. While from a broad perspective the entire region can be considered connected (Muñoz *et al.*, 2004), genetic work is showing substantial differences among the various islands even within distinct provinces or regions (Stevens *et al.*, 2006; Grobler *et al.*, 2011a; Mortimer *et al.*, 2011; Allegrucci *et al.*, 2012). Again, the genetic work is as yet insufficiently developed for formal phylogenetic approaches to the biogeography of the region to be adopted, and several questions such as the origins of the biotas of the islands of the South Indian Ocean Province (*sensu* Smith, 1984) remain unresolved. Moreover, a formal conservation planning assessment has suggested that most of the islands contribute independently to the conservation of the region and should be managed that way (Chown *et al.*, 2001). On the basis of this work and the results of the review, a list of the island groups that we suggest should be managed as separate entities is provided in Table S5 of the Supporting Information.

Marine biogeographic classifications also reveal increasing complexity through time, although distinction among areas is not always as considerable for some taxa as it is in the terrestrial realm (see Table S6 in Supporting Information). Nonetheless, taxa differ in the extent to which they reflect biogeographic disjunctions according to their dispersal ability and life history response to changes in marine conditions, in much the same way that dispersal has been found to influence patterns among terrestrial taxa occupying the Southern Ocean Islands (e.g. Clarke *et al.*, 2007; Fraser *et al.*, 2009; Wilson *et al.*, 2010; González-Wevar *et al.*, 2011; Griffiths *et al.*, 2011).

Quantitative biogeographic analyses

Environmental domains

The amount of ice-free land in each environmental domain was variable and ranged from < 1000 km^2 (domains A and G on the Antarctic Peninsula) to almost 20,000 km^2 (Transantarctic Mountains) (see Table S7 in Supporting Information). No correlation was found between area and number of biodiversity records per domain ($r_\rho = -0.43$, $P = 0.24$), but environmental favourability had an influence on record number, with most records found in the smaller, warmer domains of the Antarctic Peninsula region (Table S7). Thus, density of records was variable, ranging from 0.003 records km^{-2} in the colder Transantarctic Mountain domain to over 15 records km^{-2} in the Antarctic Peninsula offshore islands (Table S7). The Transantarctic Mountains domain represented the only spatial unit of this framework with low numbers of records; with all others having > 1000 records within them (see Fig. S5 in Supporting Information).

Using the biodiversity data partitioned into each of the nine ice-free domains, seven distinct groups were identified in the SIMPROF analyses (Fig. 3a), five of which comprised a single domain. These are D1 (Domain A – north-east tip of the Antarctic Peninsula); D3 (Domain C – southern Antarctic Peninsula); D4 (Domain D – coastal, mainly east Antarctica); D6 (Domain S – geographically disjunct areas south of the Antarctic Peninsula and in Victoria Land) and D7 (Domain R – the Transantarctic Mountains) (Fig. 3b). The other groups each comprised two domains: D2 (Domains B and G from the northern Antarctic Peninsula) and D5 (Domains T and U – a geographically disjunct set of domains around the inland coastal margins of the continent) (Fig. 3b).

Expert-defined bioregions

The expert nominal group consultation approach resulted in the identification of 33 bioregions that covered not only the continent but also the Southern Ocean Islands (SOI) (Fig. 2). At least in the latter case, these reflect some historical views on the biogeography of the SOI. To facilitate the quantitative analyses for the Antarctic continent, only the 22 bioregions that overlapped with the ice-free environmental domains were considered further. These bioregions also vary in their number of biodiversity records (see Table S8, Fig. S6 in Supporting Information), ranging from very low densities in the bioregions encompassing the Ellsworth and Transantarctic Mountains (0.003 records km^{-2}) to thousands of records in the bioregions of the Antarctic Peninsula islands (14–30.5 records km^{-2}). The highest density of records occurred in the Windmill Islands bioregion with 3446 records from an ice-free area of just 59 km^2 (58.4 records km^{-2}) (Table S8).

The SIMPROF analyses indicated that the biodiversity data currently available readily distinguish 10 distinct biogeographic regions across the continent (Fig. 3c). Only four of these groups: B1 (Bioregion M – north-east tip of the Antarctic Peninsula); B2 (Bioregion U – South Orkney Islands); B9 (Bioregion D – Marie Byrd Land) and B10 (Bioregion L – Ellsworth Mountains) represented bioregions originally defined by the expert consultation process, whereas all other groups included two or more of the pre-defined bioregions (Fig. 3d). Bioregions comprising the Antarctic Peninsula region and associated islands were clearly distinguishable from the other groups on the basis of their biodiversity. One of the most geographically disparate groupings was observed in B8, which included bioregions ranging from the southern Antarctic Peninsula through the Transantarctic Mountains and into Commonwealth Bay.

Antarctic Conservation Biogeographic Regions

Comparing the groups formed by the two cluster analyses by one-to-one matches and using the bioregion groups to partition geographically disjunct environmental domain groups, resulted in 15 Antarctic Conservation Biogeographic Regions, which are indicated on a current map of ice-free areas of Antarctica (provided by the Australian Antarctic Data Centre from the Antarctic Digital Database V5© Scientific Committee for Antarctic Research 1993–2006) (Fig. 4). Full details of the comparisons, matches and group to group partitioning are provided in Appendix S5 of the Supporting Information).

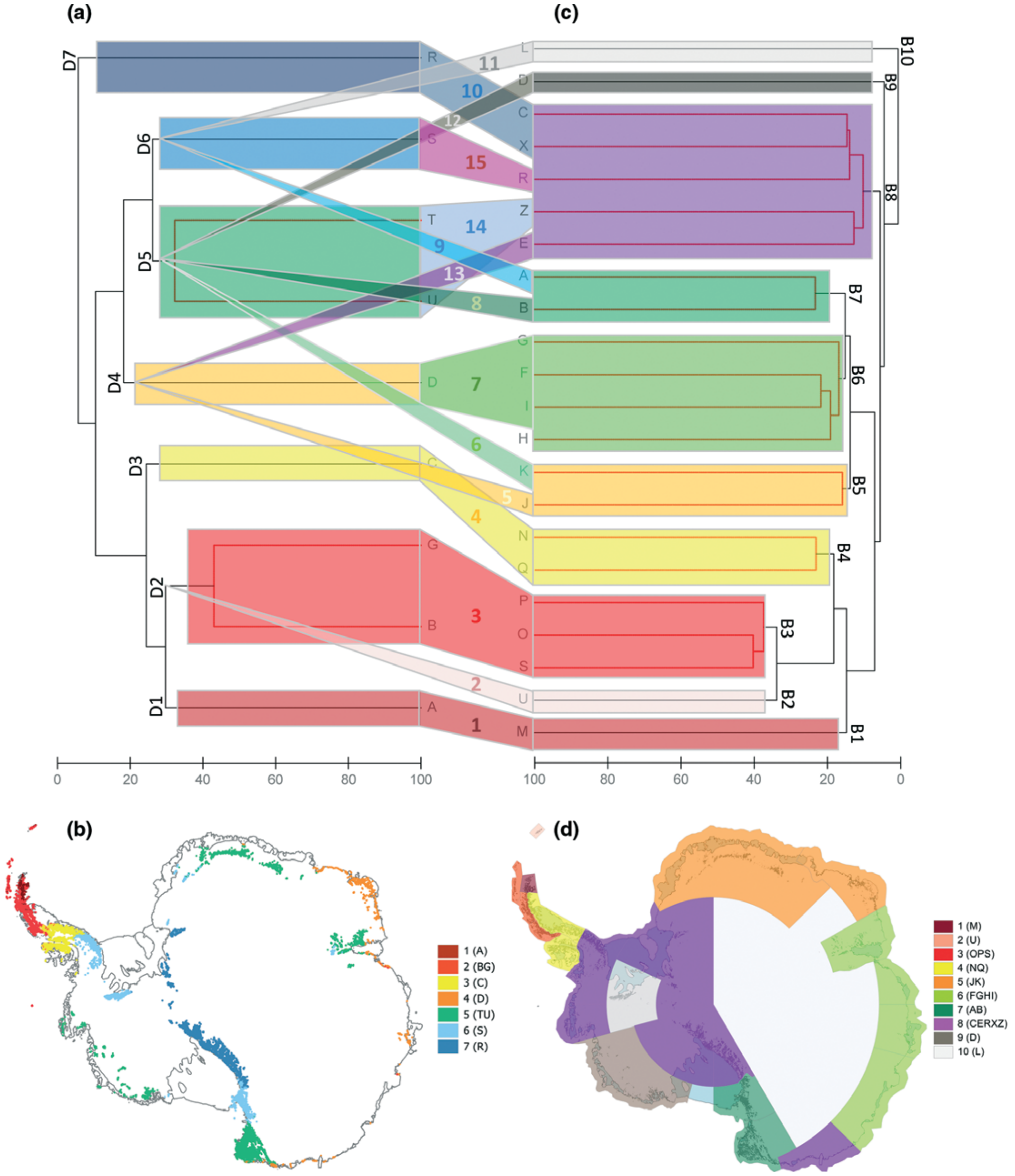

Figure 3 Cluster analyses (group averaging) and maps showing biologically distinct groups. Polygons joining two cluster show matches and bioregion groups (or parts thereof) that were used to partition domain groups. Matching polygons numbered 1–15 correspond to Antarctic Conservation Biogeographic Regions shown in Fig. 4. (a) Cluster analyses (group averaging) of environmental domains. Seven biologically distinct groups (D1–D7) identified by SIMPROF analyses have been colour coded. Red lines represent groups where there is no evidence for structure at the 5% SIMPROF significance level. (b) Ice-free environmental domain groups identified by SIMPROF cluster analyses, colour coded to match groups in (a). (c) Cluster analyses (group averaging) of expert-defined bioregions. Ten biologically distinct groups (B1–B10) identified by SIMPROF analyses have been colour coded. Red lines represent groups where there is no evidence for structure at the 5% SIMPROF significance level. (d) Groups of expert-defined bioregions identified by SIMPROF cluster analyses, colour coded to match groups in (c).

DISCUSSION

The earliest biogeographic classifications of terrestrial areas of the Antarctic region (see summary in Holdgate, 1970) tended to focus more on floristic differences (such as closed and open phanerogamic and cryptogamic communities) among areas than on the distributions of specific taxa (Table 1). The distinction among regions has continued to reflect these views and to some extent underlies differences of opinion about what the limit should be of the sub-Antarctic region (Smith, 1984). By contrast, implicit or explicit analyses of the distributions of species and/or higher taxa

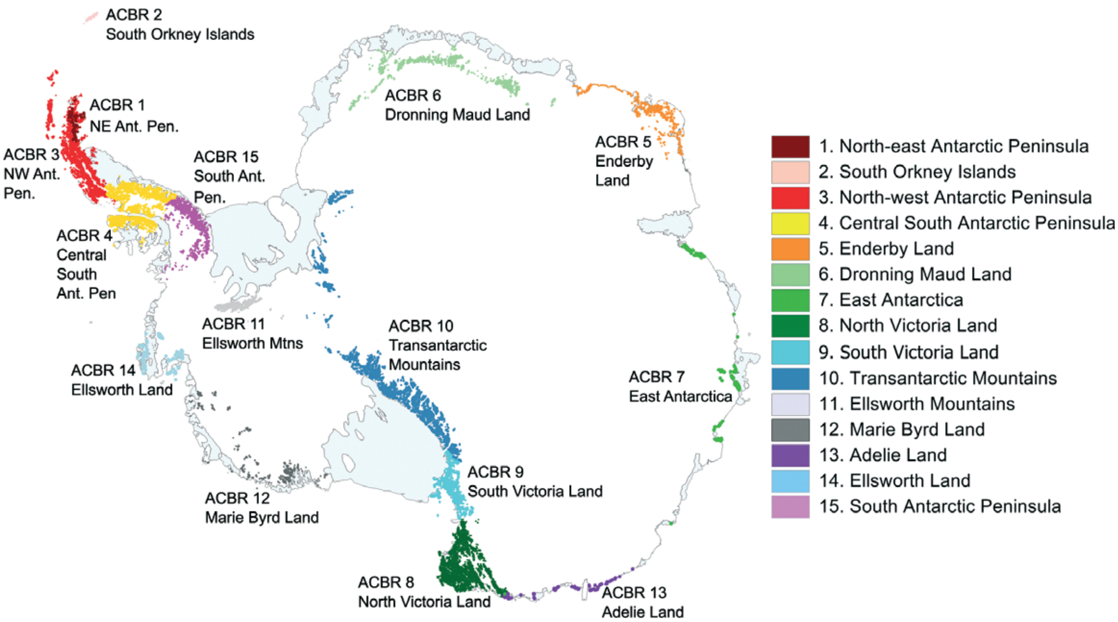

Figure 4 Fifteen Antarctic Conservation Biogeographic Regions delineated by comparing biologically distinct groups formed by the cluster analyses of environmental domains and expert-defined bioregions. Areas are based on the most up-to-date map of ice-free Antarctica (ice free layer provided by the Australian Antarctic Data Centre from the Antarctic Digital Database v5 © SCAR 1993-1996). ACBR shapefile available from Australian Antarctic Data Centre on request: http://data.aad.gov.au/aadc/biodiversity.

have emphasized that the distinctions among the cold temperate, sub-Antarctic, maritime Antarctic and continental Antarctic, and relationships among areas within these zones, tend to be dependent on the taxonomic group being investigated. This outcome reflects differences in the life histories and biologies of these groups and to some extent the current taxonomic treatment of them. For example, nestedness increases with taxon vagility in the order insects < vascular plants < land birds < seabirds, with relationships among areas (based on cluster analysis) generally reflecting the proximity of island groups to particular continents for insect and plants, but differentiation by ocean temperature for the seabirds (Greve *et al.*, 2005). For highly vagile cryptogams, one study has shown that connection by wind is a much better explanatory variable than distance to the nearest continent (Muñoz *et al.*, 2004). Thus, much of the disparity in views about the terrestrial biogeography of the Southern Ocean Islands reflects variation among the taxa investigated and the spatial scale of analysis.

Such variation is also common to the biogeography of many other areas and particularly island-type features, reflecting the fact that biogeographic patterns emerge from an interaction between the spatial structure of the environment, its evolutionary history and the life history characteristics of the organisms in question. For example, the biogeography of deep-sea hydrothermal vents reflects differences among ocean basins, rates of seafloor spreading, local turnover, and variation in the life histories and dispersal characteristics of the organisms involved (Vrijenhoek, 2010). Such variation is also reflected in the marine biogeography of the Antarctic, given that in some cases scarcely any signal of differentiation exists (Fraser *et al.*, 2009; González-Wevar *et al.*, 2011), whereas for other groups substantial biogeographic structure is present, that may also be related to temperature (Barnes & De Grave, 2001; Clarke *et al.*, 2007, 2009; Barnes & Griffiths, 2008; Griffiths *et al.*, 2011).

More recent, phylogeographic work on terrestrial organisms is reflecting the same diversity of relationships at different spatial scales depending on the taxa concerned (e.g. Myburgh *et al.*, 2007; De Wever *et al.*, 2009; Grobler *et al.*, 2011a; Born *et al.*, 2012), but importantly is also starting to provide significant insights into the origins of the biotas of various areas, and the timing of these events (Stevens *et al.*, 2006; Wagstaff & Hennion, 2007; Mortimer *et al.*, 2011; Wagstaff *et al.*, 2011). Most of these works draw attention to the significant interchanges that have taken place between Antarctica and the Southern Ocean Islands and among the islands themselves, emphasizing the biogeographic connection among these areas going back to the Miocene and Pliocene, and sometimes to earlier periods. In other words, for many terrestrial taxa, the biogeographic history of the Antarctic has not been overridden by glacial events associated with the last glacial maximum or earlier maxima (see Convey *et al.*, 2008, 2009; Hall, 2009; Bertler & Barrett, 2010; Hall *et al.*, 2010). Unfortunately, the numbers of taxa investigated to date using modern molecular phylogenetic methods is as yet insufficient to undertake the kinds of integrated biogeographic analyses that are now possible to generate and test biogeographic hypotheses (Ronquist & Sanmartin, 2011).

Nonetheless, the available information and the comprehensive analyses of the ABD undertaken here show that, while biogeographic connections among Antarctica and its surrounding islands are clear, much structure among areas exists, demonstrating that for conservation purposes areas should be managed according to a hierarchy of biogeographic differences. In other words, substantial differentiation among areas at the broadest spatial scales is clear, with further differentiation nested within specific areas, depending on the taxa concerned. For the sub-Antarctic, this is best illustrated by the Prince Edward Islands, which are sufficiently unique biogeographically (based on distribution data) to be included as an area distinct from the other islands and therefore important for conservation (Chown *et al.*, 2001), but within this archipelago again clear differences exist on a phylogeographic level among the two islands (Grobler *et al.*, 2006, 2011b), and between the eastern and western parts of the larger Marion Island (Mortimer *et al.*, 2012). The same situation is true of the Antarctic continent and its nearby islands. Our quantitative analyses of the available distribution data, based on both the environmental domains classification and on the expert-bioregions, indicate that 15 Antarctic Conservation Biogeographic Regions (ACBRs) can be readily identified (Fig. 4). These ACBRs are also broadly supported by several phylogeographic analyses, indicating substantial differences among different areas of the Antarctic Peninsula (McGaughran *et al.*, 2010; Mortimer *et al.*, 2011; Allegrucci *et al.*, 2012), among areas in Victoria Land (Stevens & Hogg, 2006; Smith *et al.*, 2010) and between East and West Antarctica (Torricelli *et al.*, 2010). Further support is provided by broader considerations of the distributions of taxa across the continent (such as indicated by the Gressitt Line, see Chown & Convey, 2007, 2012). By contrast, the ACBRs we delineate here cannot reveal local-scale phylogeographic variation (e.g. Stevens *et al.*, 2007; Hawes *et al.*, 2010).

Thus, from the perspective of the conservation management of terrestrial diversity, it is clear from our analyses and review of the current biogeographic and limited conservation planning literature for the region that at the broadest scale, each of the Southern Ocean Islands and each of the ACBRs should be managed as distinct areas of conservation significance. They should each be represented by at least one, but preferably more protected areas, and the movement of propagules among the Southern Ocean Islands and ACBRs should be limited by appropriate quarantine practices. For the Antarctic Treaty System area (i.e. south of 60°S) (Berkman *et al.*, 2011), it is clear that the numbers of Antarctic Specially Protected Areas (ASPAs – See Figure S7 in Supporting Information) varies significantly among the ACBRs, from 20 in the north-west Antarctic Peninsula (ACBR 3) to none in the Ellsworth Mountains (ACBR 11), Marie Byrd Land (ACBR 12), Ellsworth Land (ACBR 14) and the area south of the Antarctic Peninsula (ACBR 15) (Table 2, Fig. 4). In terms of area, the South Orkney Islands (ACBR 2) had the most ASPA coverage with 6.3% of their total area covered by ASPAs (Table 2). Four of the remaining ACBRs also had < 10% ASPA coverage, while 10 have < 1% ASPA coverage.

The management plans of these ASPAs, as well as the baseline terms of reference for ASPA designation specified

Table 2 Number of and area of Antarctic Specially Protected Areas (ASPAs) included within each of the Antarctic Conservation Biogeographic Regions (ACBRs).

Conservation area ID	Name	Approximate area of ACBR (km^2)*	Number of ASPAs that overlap with ACBRs†	Number of overlapping ASPAs designated for ecological reasons†	Area of ACBR that overlap with ASPAs (km^2)†	% of ACBR covered by ASPAs
ACBR 1	North-east Antarctic Peninsula	1142	1	0	0.3	0.03
ACBR 2	South Orkney Islands	148	4	4	9	6.3
ACBR 3	North-west Antarctic Peninsula	5081	20	14	231	4.6
ACBR 4	Central south Antarctic Peninsula	4959	2	1	115	2.3
ACBR 5	Enderby Land	2152	1	1	5	0.2
ACBR 6	Dronning Maud Land	5500	2	1	11	0.2
ACBR 7	East Antarctica	1085	8	7	30	2.8
ACBR 8	North Victoria Land	9522	5	3	42	0.4
ACBR 9	South Victoria Land	10368	15	9	267	2.6
ACBR 10	Transantarctic Mountains	19347	1	1	57	0.3
ACBR 11	Ellsworth Mountains	2965	0	0	0	0
ACBR 12	Marie Byrd Land	1158	0	0	0	0
ACBR 13	Adelie Land	178	3	1	0.5	0.3
ACBR 14	Ellsworth Land	220	0	0	0	0
ACBR 15	South Antarctic Peninsula	2990	0	0	0	0

*Area calculated from Lambert Equal Area projection of most recent ice-free map of Antarctica provided by the Australian Antarctic Data Centre from the Antarctic Digital Database V5© Scientific Committee for Antarctic Research 1993–2006.

†Antarctic Protected Areas Data source: Environmental Research and Assessment (2011); provided by the Australian Antarctic Division.

in the ATS, make it clear that many of them have not been established to secure terrestrial biodiversity, but have rather to protect other non-terrestrial taxa or geographical or historical features independent of biological considerations (see Table 2 and also discussion in Hughes & Convey, 2010). To what extent they can fulfil these multiple roles has yet to be determined (and is not always guaranteed, see Sinclair *et al.*, 2006 for discussion), although threats from other factors such as climate change and biological invasions are starting to be assessed (Hughes & Convey, 2010). Clearly, additional descriptions of ASPAs and further investigation of the ASPA networks' ability to represent Antarctic biodiversity is required. In the case of the restriction of propagule movements between areas, various proposals for ways in which this can be done and codes of conduct have already been drawn up (e.g. Hughes & Convey, 2010; SCAR environmental code of conduct at www.scar.org) and either accepted by the Committee for Environmental Protection of the Antarctic Treaty System (e.g. COMNAP, 2011) or are in the process of being discussed. These should be implemented and enforced for travel among islands and among ACBRs, with logistics operators providing the necessary support to ensure that these provisions can be implemented.

While we focus on the terrestrial regions of Antarctica our work is closely aligned with similar research in the surrounding marine environment. In addition to the extensive marine biogeographical work we review here, recent initiatives such as the Census of Antarctic Marine Life, which has resulted in much new spatially explicit biodiversity data for the region (e.g. AntaBIF – http://www.biodiversity.aq) and the ongoing bioregionalization work largely facilitated through Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (e.g. Raymond, 2011) are also extending our present understanding of biologically unique regions and how these might be applied to the development of marine protected areas (CCAMLR, 2011; Grant *et al.*, 2012). Future work will also focus on the nearshore benthic biogeography, which is often closely linked with the ecology of coastal ice-free areas. Conservation planning of the broader region will need to consider the biological connections between terrestrial, nearshore, pelagic and sub-Antarctic ecosystems, and the biologically different regions therein, to ensure comprehensive protection of the region's biodiversity and to maintain ecosystem functioning.

In conclusion, our work provides a novel first-tier set of sites that should form the basis of a '*systematic environmental-geographical framework*' for conservation management of the terrestrial Antarctic. It does not mean that within the ACBRs or within islands additional measures should not be established to ensure conservation of diversity and the prevention of homogenization (taxonomic, genetic, and functional). However, such measures will depend on additional information obtained at the phylogeographic level and will vary among the ACBRs and islands, as well as on the taxa concerned.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Number of records in 200-km grid cells that overlap with ice-free areas of Antarctica.

Figure S2 Relationship between number of taxa and number of records in 200-km grid cells overlaying ice-free Antarctica.

Figure S3 Dendrogram from group-average cluster analyses of 200-km grid cells.

Figure S4 Graphical output from Generalized Dissimilarity Modelling.

Figure S5 Relationship between number of taxa and number of records in environmental domains overlaying ice-free Antarctica.

Figure S6 Relationship between number of taxa and number of records in expert-defined bioregions overlaying ice-free Antarctica.

Figure S7 Location of Antarctic Specially Protected Areas.

Table S1 Number of taxa and records for each Phylum present in data set used for analyses.

Table S2 Terrestrial classification schemes of the broad Antarctic region from studies that focussed primarily on the delineation of bioregions and their relationships with each other.

Table S3 Terrestrial classification schemes of the broad Antarctic region from studies that did not focus primarily on biogeographical analyses.

Table S4 Terrestrial classification schemes of the sub-Antarctic region.

Table S5 Biogeographically distinct Southern Ocean Island groups.

Table S6 Marine classification schemes for the Antarctic and sub-Antarctic regions.

Table S7 Description of ice-free environmental domains with summary of biological records.

Table S8 Descriptions of expert-defined bioregions with summary of biological records.

Appendix S1 Exploratory analyses of 200-km grid cells.

Appendix S2 Generalized dissimilarity modelling of 200-km cells.

Appendix S3 Environmental Domains of Antarctica (EDA) analyses.

Appendix S4 List of participants in assessment of expert-defined bioregions.

Appendix S5 Details of cluster comparisons and partitioning of environmental domains by enclosing expert-defined bioregions.

Appendix S6 Supporting information references.

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BIOSKETCH

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