INFLUENCES ON AND ORIGINS OF TERRESTRIAL BIODIVERSITY OF THE SUB-ANTARCTIC ISLANDS

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(with one text-figure and five tables)

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The "sub-Antarctic" is a region of the planet characterised by small and extremely isolated island landmasses set in the vastness and harsh conditions of the Southern Ocean. Although there is no universally applicable definition of the sub-Antarctic, based on eco-climatic criteria (temperature and the presence/absence of trees or woody shrubs) a useful terrestrial biogeographic region can be defined that includes only those islands which lie close to the oceanic Antarctic Polar Frontal Zone (PFZ). These range between roughly 47°S and 54°S and include South Georgia in the South Atlantic sector of the Southern Ocean, Marion and Prince Edward islands, Îles Kerguelen and Crozet, and Heard and McDonald islands in the Indian Ocean sector, and Macquarie Island in the Pacific Ocean sector. These islands have widely differing origins and geological histories. This paper provides an overview of their biodiversity and of the major patterns in biogeography. The majority of islands are of relatively recent origin, and there are only very limited indications of a more ancient biogeographical history (Gondwana-breakup timescale) to be found in the contemporary biota. Amongst the sub-Antarctic biota, there are examples supporting two general hypotheses relating to their origin: the Insulantarctic and the multiregional scenarios. Sub-Antarctic terrestrial ecosystems, which are of biodiversity and conservation significance globally, are under considerable contemporary pressure through the twin influences of possible anthropogenic climate change, and the introduction and establishment of invasive non-indigenous species.

Key Words: biogeography, colonisation, dispersal, human impacts, climate change, South Georgia, Prince Edward Islands, Îles Kerguelen and Crozet, Heard Island, Macquarie Island.

INTRODUCTION

The "sub-Antarctic" is a region of the planet characterised by small and extremely isolated island landmasses set in the vastness and harsh conditions of the Southern Ocean. There is no universally accepted single geographic definition of the sub-Antarctic, although it is generally accepted as a meaningful term for a terrestrial biological region. For the purposes of this paper, the formulation of Smith (1984) will be used, which is based on eco-climatic criteria (temperature and the presence/absence of trees or woody shrubs), and includes only those islands which lie close to the oceanic Antarctic Polar Frontal Zone (PFZ). These range between roughly 47°S and 54°S and include South Georgia in the South Atlantic sector of the Southern Ocean, Marion and Prince Edward islands, Îles Kerguelen and Crozet, and Heard and McDonald islands in the Indian Ocean sector, and Macquarie Island in the Pacific Ocean sector. While limiting discussion here to these islands, it is only reasonable to recognise that they represent one stage of a continuum in environmental conditions between the more extreme environments of the islands and archipelagoes of the Continental and Maritime Antarctic (Balleny, Peter I Øya, South Shetland, South Orkney, South Sandwich Islands, Bouvetøya), and those of cold temperate oceanic islands and archipelagoes such as Diego Ramirez, the Falkland Islands, Tristan da Cunha, Gough Island, Amsterdam Island and New Zealand's shelf islands. Both the colder and warmer islands in these groups sometimes show considerable overlap in terms of common species or genera with those of the more tightly defined sub-Antarctic. This is demonstrated by bryophytes and lichens in relation with the maritime and continental Antarctic (Øvstedal & Smith 2001, Ochyra *et al.* in press), and by vascular plants, particularly "megaherbs", in relation with the New Zealand shelf islands (e.g., Fell 2002). In the literature, reference has been made at different times to some or all of these as "sub-Antarctic" (e.g., Dingwall 1995, Shirihai 2002).

The different sub-Antarctic islands have little in common in terms of their age and geological origin (table 1). The geological history of some areas has been contentious until recently (e.g., the Kerguelen Plateau, Wallace *et al.* 2002), and this remains the case for Îles Crozet (Craig 2003). Volcanism has been involved in the formation of many. Îles Kerguelen and Heard and McDonald islands are part of the Kerguelen Plateau, itself of Gondwanan age (although the islands are much younger) (Gladczenko & Coffin 2001). Marion and Prince Edward islands, and Îles Crozet, are shield volcanoes, which erupted 0.11–0.21 Ma and 0.2–9 Ma respectively (LeMasurier & Thomson 1990). South Georgia contains continental elements that are continuous with the Andes mountain chain of South America and the Antarctic Peninsula and Scotia Arc. Macquarie Island is an uplifted piece of largely intact seafloor ophiolite complex at the junction of the Indian-Australian and Pacific tectonic plates, and is currently thought to have emerged from the sea around 0.6 Ma (Adamson *et al.* 1995). Thus, with the exception of South Georgia, the majority of sub-Antarctic islands are substantially younger than the Southern Hemisphere continents, with the oldest being Îles Kerguelen at c. 39 Ma. Only two of the islands remain extensively glaciated today — Heard Island and South Georgia — although Pleistocene glaciation was also significant on Marion Island and Îles Kerguelen and Crozet.

The sub-Antarctic islands are often described as having "tundra" ecosystems. However, there are fundamental differences between these and the true tundra of the Arctic. These sub-Antarctic ecosystems experience a very strong oceanic influence and much reduced levels of seasonal

TABLE 1
General summary of the physical characteristics of the major groups of sub-Antarctic islands[1]

	Area (km^2)	Altitude (m)	Minimum age (myr)	Nearest continent (km)	Maximum glaciation
South Georgia	3755	2950	120	2210	complete
Marion	290	1230	0.45	1900	partial
Prince Edward	44	672	0.21	1900	no
Crozet	356	1090	0.4–8.75	2740	minor
Kerguelen	7200	1840	30	4110	almost total
Heard	368	2745	20	4570	complete
McDonald	2.6	230	0.079	5000	minor
Macquarie	128	433	0.6	990	none

[1] Data from Chown *et al.* (1998).

TABLE 2
Typical air temperature ranges experienced in summer and winter in the three commonly-recognised Antarctic and two Arctic biogeographical zones

Zone	Months with positive mean air temperatures	Mean monthly air temperature range (°C)	Extreme air temperature range (°C)	Estimate of annual degree days above 0°C (based on mean air temperatures)
High Arctic	2 to 4	–34 to +5	–60 to + 20	50–350
Low Arctic	4	–36 to + 11		600–900
Sub-Antarctic	6 to12	–2 to +8	–10 to +25	700–1700
Maritime Antarctic	1 to 4	–12 to + 2	–45 to +15	6–100
Continental Antarctic				
- coastal	0 to 1	–30 to –3	–40 to +10	0
- inland	0	<-50 to –10	<–80 to –5	0

environmental variation relative to other biogeographical regions in both the Antarctic and the Arctic (table 2). In particular this means that there is a relatively small difference between the warmest and coolest months — across all sub-Antarctic islands the warmest monthly mean temperature is only c. 7–8°C, while only those south of the PFZ (i.e., South Georgia and Heard Island) have monthly minima (slightly) below 0°C (Convey 1996a, Danks 1999). At the microhabitat level relevant to most biota, this thermal damping becomes even more apparent, with temperatures generally remaining positive year-round. Unlike the highly seasonal tundra ecosystems of the Arctic, permafrost is not present in the sub-Antarctic. An important biological consequence of these thermal regimes is that the invertebrate faunas of these ecosystems, in particular, have much reduced seasonal structure in their activity patterns and life histories (Convey 1996a, Davies *et al.* 2007). The relatively low latitude of the sub-Antarctic islands (between c. 47°S and 54°S, well north of the Antarctic Circle) also results in a longer growing season than is the case at higher latitudes (table 2), although their typically high cloud cover also reduces instantaneous radiation receipt. The islands also lie within the cyclonic belt of the Southern Ocean, experiencing typically high average wind speeds and precipitation levels.

BIODIVERSITY

The differences between levels of terrestrial biodiversity in the Arctic and sub-Antarctic are striking (tables 3 and 4), even in comparison with the environmentally much more extreme and also isolated High Arctic Svalbard and Franz Josef archipelagoes at approaching 80°N. While there are about 900 species of vascular plants in the Arctic there are only two on the Antarctic continent and a maximum of 40 on any single sub-Antarctic island (table 3). Likewise, the sub-Antarctic has no native land mammals, against the Arctic's 48 species. It is clear that the oceanic and atmospheric isolation of Antarctica and the sub-Antarctic (Barnes *et al.* 2006), in contrast with the continuous southwards continental connection of much of the Arctic, has been an important driver of the differences seen. Despite the apparent ease of access to much of the Arctic, a relatively low number of anthropogenically-introduced alien vascular plants or invertebrates are known at locations such as Svalbard (Rønning 1996, Coulson 2007), in comparison with the c. 200 species introduced to the sub-Antarctic by human activity over only the past two centuries or so (Frenot *et al.* 2005; table 5). This apparent contradiction may be explained because many of the sub-Antarctic "aliens" are cosmopolitan northern hemisphere and boreal "weeds" that have had greater opportunity to reach polar latitudes since deglaciation in the north than the south, either by natural means or during earlier phases of post-Pleistocene human colonisation.

TABLE 3
Levels of species diversity of four of the better-known groups of biota across the sub-Antarctic islands

	Higher Plants	Insects (not Collembola)	Seabirds	Land birds
South Georgia	25	21	26	2
Marion	23	19	27	1
Prince Edward	21	18	28	1
Crozet	> 19	> 44	> 33	2
Kerguelen	30	27	33	3
Heard	10	11	18	1
McDonald	5	6	9	1
Macquarie	40	20	23	0

TABLE 4
Species diversity in some of the main representative terrestrial groups of the sub-Antarctic biogeographical zone, in comparison with three Arctic locations[1]

Group	Sub-Antarctic	High Arctic (Svalbard)	High Arctic (Franz Josef Land)	Greenland
Rotifera	> 59	154		
Tardigrada	> 34	83		
Nematoda	> 22	111		
Platyhelminthes	4	10		
Annelida (Oligochaeta)	23	34		
Mollusca	3/4	0		2
Crustacea (non-marine)	44	33		65
Insecta	210	237		631
Collembola	> 30	60		41
Araneida	20	19		60
Acarina (free-living)	140	127		127
Myriapoda	3	0		1
Mammalia	0	3	2	8
Aves	0	17	6	39
Flowering plants	0	164	57	515
Bryophytes	26	373	150	612
Lichens	150	597	> 100	950

[1] Data sources: Svalbard – Barr (1995), Elvebakk & Hertel (1996), Frisvoll & Elvebakk (1996), Rønning (1996), Coulson & Resfeth (2004), Coulson (2007); Franz Josef Land – Barr (1995); Greenland – Jensen & Christensen (2003); sub-Antarctic – Convey (2007a).

TABLE 5
The recorded occurrence of alien non-indigenous species across Antarctic biogeographical zones[1]

	Continental Antarctic	Maritime Antarctic	Entire sub-Antarctic	South Georgia	Marion	Prince Edward	Crozet	Kerguelen	Heard	Mac Donald	Macquarie
Dicotyledons	0	0	62	17	6	2	40	34	0	0	2
Monocotyledons	1	2	45	15	7	1	18	34	1	0	1
Pteridophytes	0	0	1	1	0	0	1	1	0	0	0
Total non-indigenous plants	0	2	108	33	13	3	59	69	1	0	3
Invertebrates	0	2–5	72	12	18	1	14	30	3	0	28
Vertebrates	0	0	16	3	1	0	6	12	0	0	6

[1] Extracted from Frenot *et al.* (2005) and Convey (2007b); see also Greenslade (2006) for a detailed description of established and transient alien species, and species recorded only synanthropically, from sub-Antarctic Macquarie Island.

Sub-Antarctic floras and faunas are typically disharmonic and do not include representatives of several taxonomic and functional groups common in lower latitudes. Sub-Antarctic plant communities do not include woody plants, and are dominated by herbs, graminoids and cushion plants. These floras also generally do not include species requiring insect pollination, other than possibly two little-known endemic orchid species from Macquarie Island, and pollinating insects likewise do not form a component of the insect faunas (Convey *et al.* 2006a). Megaherbs are a striking element of the flora of many islands, being an important structuring force within habitats, and a major contributor of biomass (Meurk *et al.* 1994a, Mitchell *et al.* 1999, Fell 2002, Shaw 2005, Convey *et al.* 2006a). Several different plant families are represented by regional and endemic megaherb taxa (Apiaceae – *Stilbocarpa*, Brassicaceae – *Pringlea*, Asteraceae – *Pleurophyllum*). Large tussock grass species (Poaceae – *Poa* and *Parodiochloa*) also provide a dominant structural presence. These plant growth forms present an unusual combination of morphological and life history characteristics (Convey *et al.* 2006a), that includes high primary production and biomass allocation to both leaf and underground storage tissue, seed mass and seed output. Their dominance on sub-Antarctic islands is thought to have been encouraged by the absence of natural vertebrate herbivores (Meurk *et al.* 1994a, Mitchell *et al.* 1999), while also having other adaptive benefits relating to the harvesting and focusing of low light levels and aerosol nutrients (Wardle 1991, Meurk *et al.* 1994b). The recent anthropogenic introduction of vertebrate herbivores to most sub-Antarctic islands has led to considerable and negative impacts on megaherb-based communities (Frenot *et al.* 2005, 2007, Shaw *et al.* 2005, Convey *et al.* 2006b).

Across the sub-Antarctic there are no native land mammals, reptiles or amphibians and very few non-marine birds. The latter are limited to three species of freshwater duck (two on South Georgia, one on Îles Kerguelen and Crozet), a single passerine endemic on South Georgia (*Anthus antarcticus* Cabanis, 1884 the South Georgia Pipit), and two scavenging sheathbills. Although outside the scope of this review, many of the islands are of considerable conservation importance, hosting globally significant populations of marine vertebrates (Woehler *et al.* 2001). The most abundant macroscopic terrestrial invertebrates of the sub-Antarctic are the micro-arthropod mites and springtails, with population densities in tens to hundreds of thousands of individuals m^{-2}. There are also enchytraeids, earthworms, tardigrades, nematodes, spiders, beetles, flies and moths, with smaller representation of some other insect groups (Gressitt 1970, Convey 2007a). Few of these invertebrates are thought to be true herbivores, with the exception of some beetles and the moths, although detailed autecological studies are typically lacking. Spiders and a small number of carabid, dytiscid and staphylinid beetles are carnivorous but, other than these, macro-invertebrate predators are absent, and predation levels are thought to be insignificant (although this is a generally untested assumption). The introduction of carabids to parts of South Georgia and Îles Kerguelen is leading to extensive changes to local community structure, which threaten the continued existence of some indigenous and/or endemic invertebrates (Ernsting *et al.* 1995, Frenot *et al.* 2005, 2007). Regional warming has also been predicted to rapidly increase the impact of certain indigenous predators, such as the diving beetle *Lancetes angusticollis* (Curtis, 1839) in lakes on South Georgia (Arnold & Convey 1998). Despite the preponderance of detritivores, decay processes are slow in most habitats. Detailed studies on Marion Island have indicated that indigenous detritivorous invertebrates are currently insufficient to overcome a bottleneck in the decomposition cycle (Slabber & Chown 2002).

Although sub-Antarctic ecosystems are more diverse and complex than those of more extreme Antarctic latitudes (Convey 2007a), they remain simple in global terms, commonly lacking or with low diversity in specific taxonomic or biological functional groups. Therefore they are thought to lack the functional redundancy that is typical of more diverse ecosystems. This lack of indigenous diversity raises the possibility of new colonists (natural or anthropogenically-assisted) filling previously unoccupied ecological niches. Such colonists could include new trophic functions or levels, and would inevitably change fundamentally the structure and function of trophic webs. Responses of indigenous biota to such changes and the advent of new competitors and predators will be constrained by their typically "adversity-selected" life history strategies (Convey 1996b), which primarily confer abilities to survive abiotic environmental extremes, while competitive abilities are very poorly developed. These native species and communities appear to be particularly vulnerable to predation from invading taxa, as native invertebrate predators are generally of little or no significance (Ernsting *et al.* 1995, Convey 1996b, 2003, Frenot *et al.* 2005, Convey *et al.* 2006b).

BIOGEOGRAPHIC PATTERNS AND DRIVERS

The widely varying geological and glaciological histories of the sub-Antarctic islands provide the template on which their patterns of biodiversity and biogeography have evolved. Understanding of these patterns relies on resolution of three fundamental problems: (1) many areas have not been systematically explored, even on such defined and small land masses; (2) many of the less charismatic taxa have not received basic survey attention even for those that have, and comprehensive and up-to-date databases of the distributions of sub-Antarctic species do not exist; (3) both robust systematic studies and modern molecular phylogenies are absent for many taxa, while very few taxonomists or funding agencies have resources to devote to the biota of this region. Although a number of recent compilations are available either for specific islands or specific taxonomic groups, both of published records and of newly (re-)examined material (Pugh 1993, Bednarek-Ochyra *et al.* 2000, Øvstedal & Smith 2001, Pugh *et al.* 2002, Pugh & Scott 2002, Seppelt 2004, Chown *et al.* 2006, Greenslade 2006, Ochyra *et al.* in press), these factors mean that any biogeographic assessments inevitably rely on incomplete data and, hence, are constrained to weak approaches to phylogeographic analyses (Chown & Convey 2006, 2007). For instance, the closest relatives of many prominent endemic sub-Antarctic invertebrate taxa (the *Ectemnorhinus*-group weevils and *Pringleophaga* spp. tineid moths) remain unconfirmed except on the basis of conventional systematics (Jeannel 1964, Kuscbel & Chown 1995). Using the available data, Chown *et al.* (1998) identified that several well-known biodiversity drivers were important across the Southern Ocean islands, including area, distance from sources, temperature, richness of other biotic groups and human occupancy (see also Selmi & Boulinier 2001).

Perhaps the most fundamental challenge relating to sub-Antarctic terrestrial biogeography is that of separating the two influences of dispersal and vicariance in determining the current distributions across the region. This dichotomy is superimposed on a second area of controversy, that of whether the entire sub-Antarctic region can be regarded as a single biogeographic province (the "Insulantarctic" hypothesis – Udvardy 1987), or whether a "multiregional" hypothesis is more appropriate (i.e., that there are different provinces of the Southern Ocean, with different origins, history and sources of biota – Kuschel & Chown 1995, Craig *et al.* 2003). The debate essentially rests on whether all the islands share enough of their biotas to form a single biogeographic entity (as proposed by Holdgate 1960, Skottsberg 1960, Udvardy 1987, van de Vijver & Beyens 1999), or whether there are sufficient regional differences simply to require that each is most appropriately linked to the Southern Hemisphere continent to which they are closest (Gressitt 1970, Smith 1984, Morrone 1998, Cox 2001, McDowall 2005).

In many respects this is a sterile debate (Chown & Convey 2006), with the conclusion drawn depending to a large extent on the particular taxonomic group under consideration (Greve *et al.* 2005). The latter authors present evidence, based on the degree of nestedness shown in distributions of species and genera of different groups, that illustrates instances of support for both the Insulantarctic and multiregional hypotheses. Distribution patterns of groups that are weak dispersers are strongly influenced by regional source pools, in particular the most adjacent continents and large islands within archipelagoes (Morrone 1998), whilst those of mobile taxa (i.e., those with dispersing life stages) are more uniform (Barrat & Mougin 1974). A number of very different organisms (oribatid mites – *Halozetes*, springtails – *Cryptopygus*, grass – *Deschampsia*, herb – *Acaena*) share circum-sub-Antarctic distributions (Bergstrom *et al.* 2006; illustrated in fig. 1 for *Acaena*), which are most parsimoniously explained by dispersal processes acting across the entire region. However, there remain important anomalies. For instance, bryophytes are widely regarded as efficient dispersers, producing a range of spores and other propagules (Longton 1988). Of the terrestrial biota of the Antarctic continent bryophytes are the only major group present to show the very low levels of species endemism that should be associated with the widely assumed pattern of recent (post-Pleistocene glaciation) colonisation (Chown & Convey 2006, Peat *et al.* 2007, Convey *et al.* in press b). However, while Muñoz *et al.* (2004) proposed that sub-Antarctic bryophyte distribution patterns support an hypothesis of dispersal by wind across the region, nestedness analysis suggested little difference was present in reality between them and what are highly

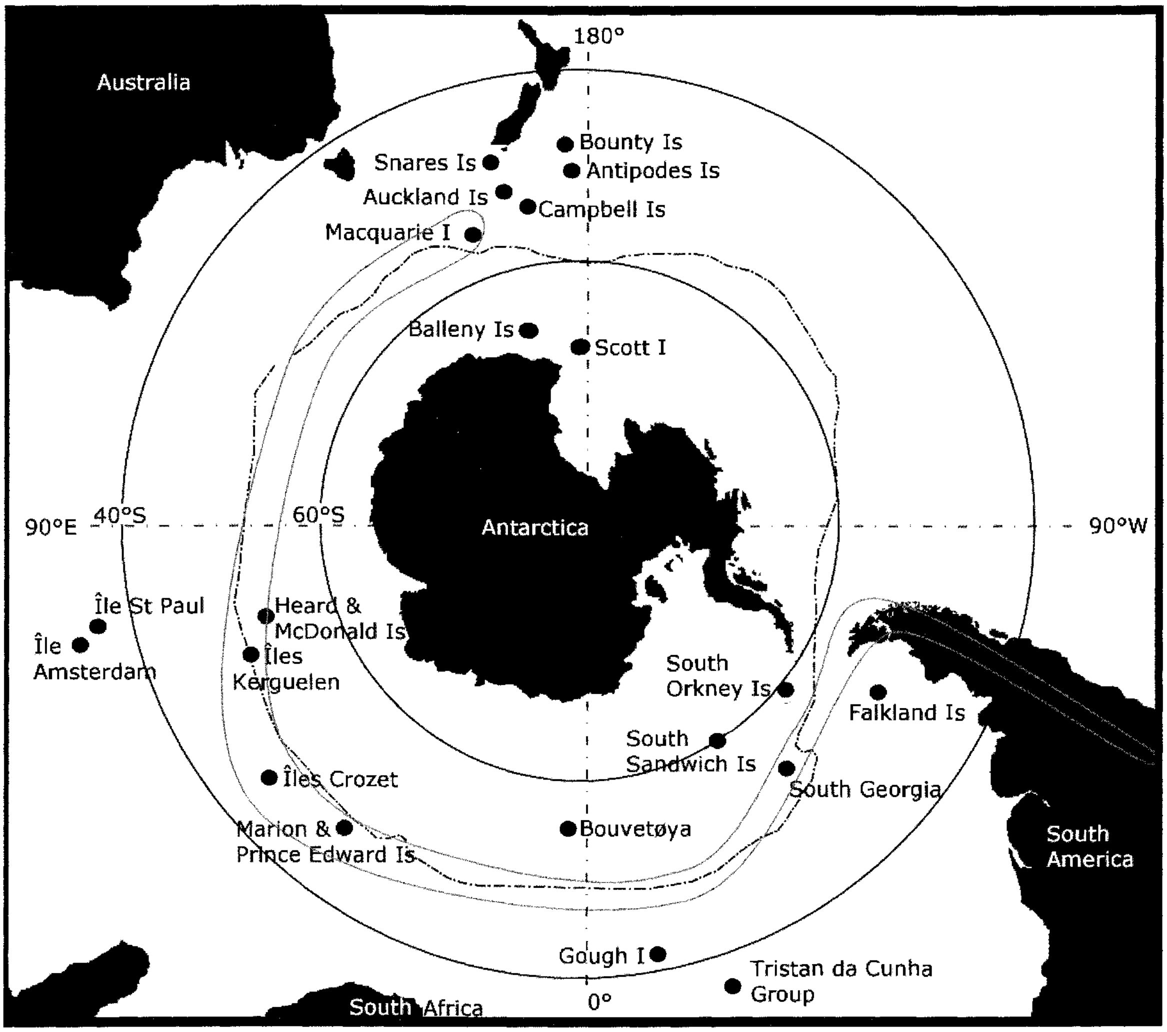

FIG. 1 — The circum-Antarctic distribution of the herb Acaena *(reproduced from Bergstrom* et al. *2006).*

regionalised vascular plant distributions (Greve *et al.* 2005). This contradiction may relate in part to the use of imperfect taxonomy in the earlier study, but it may also illustrate that long-range bryophyte dispersal may not be as effective as is commonly assumed.

While the majority of islands are too young to carry a signal of their biological history on a Gondwana-breakup timescale, the older islands of South Georgia and Kerguelen have the potential to do so. However, terrestrial fossil evidence is generally sparse in the sub-Antarctic, other than fossil floras that are known from islands of the Kerguelen Plateau (Chastain 1958, Quilty & Wheller 2000; Truswell *et al.* 2005) and a single example of fossil wood, dating from the Early Cretaceous, from South Georgia (Gordon 1930). Nothing can be concluded about continuity between fossil and contemporary biota. Other studies have inferred signals of ancient regional origin from contemporary distributions (Brundin 1966, Darlington 1970, McInnes & Pugh 1998, Craig 2003). An example of this is provided by the Collembola genus *Setanodosa*, known only from South Georgia in the Antarctic/sub-Antarctic region, and from South America, South Africa and Australia. The implication is of a Gondwanan distributional link, at least between the major continents, although in the absence of molecular phylogenetic studies it is not currently possible to differentiate between this and more recent dispersal in explaining the presence on South Georgia.

A single molecular phylogenetic study of Scotia Arc Diptera has proposed the continuous presence of an evolutionary lineage of chironomid midge on the South Georgian microplate over a timescale dating from its separation from southern South America and the Antarctic Peninsula (Allegrucci *et al.* 2006), 40–50 ma. Also based on molecular phylogenetic analyses, Stevens *et al.* (2006) inferred recent (<2 ma) dispersal/colonisation events of springtail (*Cryptopygus*) species between some sub-Antarctic islands, with a close association between estimated times of divergences based on a molecular clock and proposed geological ages of islands. On a more recent timescale, local isolation of populations by Pleistocene glacial cycles has been an important evolutionary force driving differentiation processes (Marshall & Convey 2004, Mortimer & Jansen van Vuuren 2007). These studies demonstrate the potential for the application of such techniques to shed light on the biogeographical history and structure of the sub-Antarctic, and rapid advances are now being made in this field.

Ignoring for the moment the direct influence of humans, there are three broad mechanisms that might facilitate natural colonisation and dispersal processes into and within the Antarctic (Gressitt 1970, Hughes *et al.* 2006). These are transport in air, water or via a third-party vector (other organisms, debris). Wind is well known to play a major role in the colonisation of isolated environments by smaller organisms, particularly those with an appropriate stress-resistant life stage. In a sub-Antarctic and Antarctic context, this applies to bryophytes, lichens, many microbes and certain invertebrates such as rotifers, tardigrades and some freshwater crustaceans and terrestrial arthropods (Laybourn-Parry & Marchant 1992, Marshall 1996, Muñoz *et al.* 2004, Greve *et al.* 2005). However, it is also currently thought that long-distance aerial dispersal is inappropriate for other elements of the sub-Antarctic and Antarctic faunas, such as most terrestrial arthropods and molluscs (Pugh & Scott 2002, Pugh 2003), while it may only operate on relatively short scales of distance for others such as Collembola (Hawes *et al.* 2007b). Other than the study of Marshall (1996), which relates to a maritime Antarctic island location, there are no recent studies quantifying the frequency or magnitude of aerobiological transfer into the Antarctic region. However, it is clear from the occasional arrivals of known migratory moth species that aerial transfer to the sub-Antarctic islands does occur (Greenslade *et al.* 1999, Convey 2005).

Given the scale of physical isolation of the sub-Antarctic islands, and the typical meteorological conditions and sea states experienced at their latitudes in the Southern Ocean, transport in water or on the water surface would seem unlikely, and there are no confirmed instances. However, some groups well-represented in sub-Antarctic terrestrial faunas, such as the ameronothroid mites and some isotomid and hypogastrurid springtails, are known to show very wide ecophysiological tolerances and can survive long periods in or on the surface of seawater (Strong 1967, King *et al.* 1990, Davenport & MacAlister 1996, Coulson *et al.* 2002, Marshall & Convey 2004, Hawes *et al.* 2007a). This mechanism is likely to underlie dispersal of marine littoral species, some of which also then occupy supralittoral habitats. There are also no demonstrations of transfer of terrestrial species into or within the Antarctic region on floating debris, although the possibility has been recognised and examples relating to marine biota exist (Barnes & Fraser 2003, Hughes *et al.* 2006).

Finally, the potential route of zoochory (transport attached to other animals, usually vertebrates) has been recognised (Pugh 1997) although, again, there are few confirmed examples of this occurring in the Antarctic or sub-Antarctic. Earlier reports are limited to algae and microbiota (Gressitt 1964, Schlichting *et al.* 1978). Recently, Krivolutsky *et al.* (2004) have carried out a more detailed study of the arthropod load carried by a range of Antarctic bird species collected on the South Shetland Islands and Antarctic continent. They report several species of mite and a single spider being collected from the plumage of these birds, none of which were apparently species resident at the collection locations. Perhaps most surprisingly, species thought to be terrestrial were collected from the plumage of penguins, including from Emperor Penguins that do not come into direct contact with terrestrial habitats at any point in their life-cycle. In a sub-Antarctic context, the most plausible bird vector species are those that routinely migrate to other continents (skuas, gulls and sheathbills) (Barnes *et al.* 2006). In some cases, some invertebrates and plant and microbial propagules may possess appropriate resistance features to permit survival of passage through vertebrate guts (Frenot *et al.* 2005), such as those of seals (Pugh 1994) and sub-Antarctic ducks (T. Martin, pers. comm.).

HUMAN IMPACTS

Antarctica and the isolated lands of the Southern Ocean are unique in never having had an indigenous human population or a long-term history of human residence and impact. The short human history in the region commenced with early exploring voyages into the Southern Ocean, and with the discoveries of the isolated peri-Antarctic islands, within the past two to three centuries. The Antarctic Peninsula (West Antarctica) was first sighted in 1820, and probably landed on in 1821, and humans first set foot on East Antarctica in 1895 (Headland 1989). Direct human impacts so far have largely been restricted to Southern Ocean marine ecosystems (sealing, whaling, fishing) and sub-Antarctic terrestrial ecosystems (Knox 1994, Frenot *et al.* 2005, 2007, Convey *et al.* 2006b, in press a). Indirectly, human activities are also impacting the Antarctic through the pervasive presence of persistent organic and inorganic pollutants (Bargagli 2005), and the processes of climatic change consequential on global warming and stratospheric ozone depletion (Walther *et al.* 2002, Convey 2003, 2006). Human contact with Antarctica is currently growing rapidly (Navareen *et al.* 2001, Frenot *et al.* 2005, COMNAP 2006, IAATO 2006). Identifying and responding to the requirements for conservation of Antarctic ecosystems are high profile issues both within the Committee for Environmental Protection of the Antarctic Treaty System, and within the sphere of public interest generated through the media and activities of non-governmental organisations.

Parts of the Antarctic region are currently experiencing rapid change in a number of climatic variables – most obviously temperature, but also in precipitation patterns and amounts, and cloudiness. Some of the most rapid temperature increases seen worldwide over the past 50 years have been documented along the western Antarctic Peninsula and associated Scotia Arc archipelagoes (King *et al.* 2003, Vaughan *et al.* 2003, Turner *et al.* 2005). Although the only sub-Antarctic island included in this region is South Georgia, the maritime Antarctic island archipelagoes are also included; some authors group these with the more strictly defined sub-Antarctic islands. Warming trends have also been identified at several other sub-Antarctic locations (Jacka & Budd 1998, Marion Island - Smith & Steenkamp (1990), Smith (2002), Îles Kerguelen - Frenot *et al.* (1997), Macquarie Island - Tweedie & Bergstrom (2000)). At finer, seasonal, timescales as yet there are no consistent seasonal patterns across the sub-Antarctic islands. Thus, Macquarie Island appears to be warming most during late summer and early autumn (Adamson *et al.* 1988), although this was not confirmed by Tweedie & Bergstrom (2000). Highest warming rates are seen on Marion Island during late winter and early summer (Smith & Steenkamp 1990). There is some evidence that Îles Kerguelen are warming more in summer (Allison & Keage 1986; but see also Frenot *et al.* 1997 who reported no seasonal difference in a longer dataset). Precipitation patterns are also changing on some islands, with reports of both increases on Macquarie Island (C. Tweedie, D. Doley & D. Bergstrom unpublished data), and decreases on Marion Island and Îles Kerguelen (Smith & Steenkamp 1990, Frenot *et al.* 1997, Chown & Smith 1993, Smith 2002, Chapuis *et al.* 2004). In concert with these changes, rapid rates of glacial retreat have taken place on the heavily glaciated South Georgia and Heard Island (Gordon & Timmis 1992, Pugh & Davenport 1997, Kiernan & McConnell 2002). This process has various consequences, including exposing new ground for colonisation, altering (generally increasing) water input to terrestrial habitats, and opening up overland routes for movement of terrestrial biota into previously isolated regions. The latter is of particular significance for South Georgia, as it permits the movement of introduced rats and reindeer into new areas, with highly deleterious consequences for native ecosystems (Frenot *et al.* 2005, Convey *et al.* 2006b).

The consequences of changes in two major environmental variables (temperature, water availability) have formed a particular focus in studies of climate change responses in the Antarctic, although few such studies have focused specifically on the sub-Antarctic islands. The widely reported warming trends have led to a range of general predictions (Convey 2003), including increases in the rates of colonisation on both local and long-distance scales, increased terrestrial diversity and biomass, and increased trophic complexity (through the inclusion or greater functional representation of higher trophic levels). As yet, few studies have addressed these processes in a sub-Antarctic context, although environmental manipulation studies on South Georgia (Smith 2001) have demonstrated local colonisation and community development potential through dormant propagule banks. Negative consequences from environmental changes are also clearly possible, and one such might be a reduction in local extent of *Azorella* cushion plants on Marion Island, influenced by the trend of reduced precipitation recorded on this island (le Roux *et al.* 2005).

Human contact with the sub-Antarctic over the past two centuries or so has led to the introduction of over 200 known non-indigenous species (table 5; Frenot *et al.* 2005). The majority of these are vertebrates or flowering plants, although an increasing number of invertebrates are now being recognised (Greenslade 2006). However, it remains the case that the quality of data available varies widely between the sub-Antarctic islands and also between the major higher taxonomic groups. Thus, while the presence of non-indigenous flowering plants is quite well known throughout the region, little or no attention has been given to bryophytes or lichens. Likewise, detailed data are unavailable for most microarthropod and other microfaunal groups (nematodes, tardigrades, rotifers), to the extent that even authoritative lists of indigenous species are not available in many cases, rendering the identification of non-indigenous species problematic (although see Greenslade (2006) for Macquarie Island). However, it is clear that some major sub-Antarctic islands remain relatively unaffected by the establishment of non-indigenous species (particularly Prince Edward and Heard islands). The value and conservation status of these two islands has been recognised by, in the former case, the operation of a detailed and proscriptive management plan (Anonymous 1996), and in the latter by the awarding of World Heritage Site status (see Chown *et al.* 2001). However, other sub-Antarctic islands have been and continue to be heavily impacted (particularly South Georgia, Îles Kerguelen, Macquarie Island). On these islands there have been well-documented examples of drastic ecosystem impacts, mainly relating to rodent or cat predation of indigenous birds, mammalian grazing, and the spread of cosmopolitan weed plant species (see Frenot *et al.* (2005) for review). Because some of the impacted species and ecosystems are very restricted globally, damage to these islands presents an important threat to regional and global biodiversity. Although natural colonisation of the species-poor sub-Antarctic ecosystems is an ongoing process, the importance of anthropogenic activity in facilitating introduction and establishment must also be recognised. Studies on sub-Antarctic Marion Island and South Atlantic Gough Island suggest that the frequency of anthropogenic introduction outweighs that of natural processes by up to two orders of magnitude or more (Gaston *et al.* 2003, Gremmen & Smith 2004, Pugh 2004). After only two centuries of contact, anthropogenic introductions now account for over 50% of angiosperm biodiversity on South Georgia and Îles Kerguelen. Non-indigenous species that become invasive are now presenting major challenges for ecosystem management, and in most cases no simple solutions are available. Even in cases where eradication of introduced species is practicable (most obviously, grazing large mammals and cats), it is not clear that eradication will simply lead to ecosystem recovery.

CONCLUSIONS

A number of formulations or definitions of the sub-Antarctic are in more or less common use in the literature. The definition used in the current paper, based on climatic similarities and the common absence of woody plants, identifies a discrete set of isolated Southern Ocean islands at latitudes of c. 47°S to 54°S, all lying relatively close to the oceanic PFZ. Terrestrial ecosystems on the majority of these islands are plainly post-Gondwanan in origin, as most islands formed long after Gondwana-breakup. A few (particularly South Georgia) provide evidence of ancient biogeographical signals consistent with events during the final breakup of Gondwana. The extreme isolation and generally poor environmental conditions experienced in this region are indicated by the overall low levels of biodiversity present on all islands, and their disharmonic taxonomic composition. Contemporary biogeographical patterns vary between groups of biota or habitats, with examples supporting both Insulantarctic and multi-regional hypotheses for their origin, and strong indications of both the importance of wind and other means of long-distance dispersal as well as of more local evolutionary radiation. Recent human impacts (climate change, introduced species) are already strong, and may far outweigh natural dispersal processes, presenting major management and conservation challenges.

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