TRENDS IN ANTARCTIC TERRESTRIAL AND LIMNETIC ECOSYSTEMS

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Antarctica as a Global Indicator

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Cover Illustration: Back ground photo: Nunataks in the Behrendt Mountains, Ellsworth Land, continental Antarctica, host some of the simplest terrestrial faunal communities known on the planet. *Photograph: Pete Convey.*

Insert photo: Eight invasive mammals are currently established on subantarctic islands. Other than rodents, the remainder were originally deliberately introduced by humans. Cats are responsible for drastic reductions in some seabird populations. This photograph shows a cat in a king penguin colony in the Iles Kerguelen. *Photograph: Jean-Louis Chapuis.*

Steven Chown (South Africa) has rolled across a cushion plant vegetation on Heard Island (subantarctic, Indian Ocean sector) as to not damage it, in order to sample arthropods from *Pringlea antiscorbutica* (Kerguelen cabbage). Note: there are no footprints. *Photograph Dana Bergstrom*.

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PREFACE

Motivated by the Northern Hemisphere International Tundra Experiment (ITEX), Dana Bergstrom instigated a workshop in Brisbane, Australia, in 1998 to discuss the concept for a Southern Hemisphere ITEX using a series of networked sites in and around Antarctica. Instead of following the ITEX model of looking at variations in organismal performance with longitude, the new program would be based around the premise that latitude and altitude could act as proxies or predictors for future climate change. Using the power of the internet, these concepts and intentions were disseminated to researchers who formed various discussion groups. There were instant replies from Ad Huiskes and Burkhard Schroeter in Europe, who exclaimed that they had conceived a similar concept while tent-bound in a blizzard on the Antarctic Peninsula.

Thus began the SCAR program, Regional Sensitivity to Climate Change in Antarctic Terrestrial and Limnetic Ecosystems (RiSCC). An initial workshop was hosted by Antonio Quesada and Leo Sancho, with support from the Spanish Antarctic Program, to further develop the concept. This was followed by a science planning workshop, hosted by Steven Chown in South Africa. These workshops defined the foundations for the RiSCC Program, which were to study changes and patterns in species diversity and organismal performance around Antarctica. The data collected were to be linked with latitude along the "Antarctic Environmental Gradient", which extends over 40° of latitude from Marion Island at 47ºS to the Transantarctic Mountains at 87ºS, and includes a range of climatic zones present on the cool temperate oceanic islands to the frigid and arid Antarctic continent.

RiSCC ran for just over five years (2000–2005), before being absorbed within the new framework of SCAR international scientific programs, and contributing to the development of its successor program "Evolution and Biodiversity in Antarctica". Without a doubt, RiSCC has been a very successful enterprise and catalyst when seen from a number of perspectives: almost 200 peer-reviewed scientific publications have emerged from the scientific activities associated with the program, a strong international science network has developed with the active involvement of scientists from over 18 nations, and RiSCC proved the nexus for several successful international expeditions.

RiSCC has helped to improve our understanding of the interactions and linkages among climate change, indigenous and alien species, and the ways in which ecosystems function. This volume is a culmination of the efforts and findings of the RiSCC community. We would like to thank all our authors for their efforts, and the members of the RiSCC program in general whose scientific findings are reported here. We thank all referees for their prompt efforts to provide sage advice on all chapters in this volume. We would also like to thank Eric Woehler for his enormous efforts in helping us get the book to publication. Eric has filled numerous roles including sub–editor, illustrator and tireless supporter of the project, and has dedicated five months of his life to this cause.

We dedicate the book to one of the original RiSCC ‘Three Musketeers’, Burkhard Schroeter, who while no longer pursuing his passion for Antarctic field research, now perhaps has a far more important role in life, that of teaching and inspiring the next generation of scientists.

Dana Bergstrom, Pete Convey and Ad Huiskes (eds).

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1. TRENDS IN ANTARCTIC TERRESTRIAL AND LIMNETIC ECOSYSTEMS: ANTARCTICA AS A GLOBAL INDICATOR

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Introduction

The Antarctic provides a suite of environments and scenarios that give key opportunities to improve understanding of the consequences of climate change on terrestrial and limnetic biota. These result both from the considerable differences in the rates of contemporary change in the region, and the marked natural environmental gradients present in terrestrial and limnetic ecosystems. Antarctic communities range from polar deserts and permanently frozen lakes to lush,

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eutrophic grasslands and nutrient-enriched ponds. Such gradients, including latitudinal, altitudinal and environmental examples, provide useful analogues for the predictions of future change trajectories. Regional differences in the nature of the changes currently experienced add a further, useful, layer of complexity. For instance, strong seasonal differences in the rate of temperature change are seen in the Antarctic Peninsula region, with autumn and winter temperatures having increased substantially more than those in the spring and summer. Precipitation rates in the Peninsula area are also predicted to increase, whereas they have been decreasing dramatically on several subantarctic islands.

The international research programme RiSCC (Regional Sensitivity to Climate Change in Antarctic Terrestrial and Limnetic Ecosystems), sponsored by the Scientific Committee on Antarctic Research, has been investigating these scenarios with the goals of (1) understanding the likely response of Antarctic biotas to changing climates and (2) contributing to the development of broadly applicable theory applying to interactions among climate change, indigenous and introduced species and ecosystem functioning. The purpose of this volume is to provide a picture of the current state of knowledge of the Antarctic terrestrial and limnetic ecosystems and a synthesis of the known and likely effects of climate change on Antarctic terrestrial and limnetic ecosystems, based on data gathered by the RiSCC programme and from the wider literature and, thereby, to contribute to their management and conservation. In doing so, we also highlight the global significance of developing understanding of climate change consequences in the Antarctic. Rates of change currently seen in this region are amongst the greatest documented worldwide, while overall knowledge of the relatively simple ecosystems is often more developed, allowing the region to act as a "canary in the coalmine" for planet Earth (Convey et al. 2003).

Antarctic opportunities

Antarctica[1] has long been described as the most remote continent on Earth, the last true wilderness, unspoilt by humans, and isolated from external environmental influences by the Polar Vortex in the upper atmosphere and the Antarctic Polar Front in the Southern Ocean. To the uninitiated, Antarctica is a hostile place, cold and windy, covered in ice and inhabited only by seabirds and mammals. It is familiar to most through media reports and television programmes, made by those few who venture there.

However, in the last few decades scientists have come to appreciate that the continent is fundamental to global processes. Furthermore, the continental icecap, averaging over 2km and up to 5km deep, contains an unique archive of the atmospheric composition at least over the last 800 000 years (EPICA 2004), trapped in air bubbles in the ice. This archive is of vital importance in the reconstruction of

[1] We use the term 'Antarctica' to refer to the continent in a geographical sense, and "the Antarctic" in a biogeographical sense, *ie* including the subantarctic islands.

climate evolution and climate fluctuation and allows the reconstruction of past climate fluctuations and refining of scenarios for future climate change. On even longer timescales, the geology of the continent provides information on past climate evolution and on the causes, mechanisms and timescales of the fragmentation of the supercontinent Gondwana.

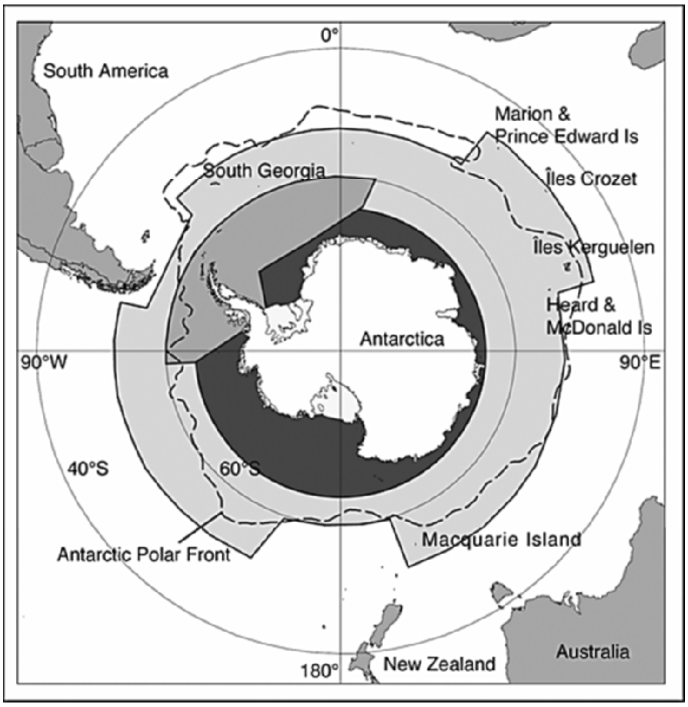

Figure 1. Map of Antarctica with the surrounding subantarctic islands. Dark shading indicates continental Antarctica, medium shading the maritime Antarctic and light shading the subantarctic region.

Looking inwards towards the Antarctic, external influences on the Antarctic environment and its biome have long been considered negligible or at most only of local importance. As late as 1985 Phillpot advocated "…caution in suggesting the possibility of 'climatic change'…" in connection with Antarctica (Phillpot 1985). Twenty years later, we are fully aware of the fact that Antarctica is not the remote continent we once thought. Anthropogenic chlorofluorocarbons (CFCs) and CO_2 and other greenhouse gases, released into the atmosphere mainly in the Northern Hemisphere, exert a profound influence on the global atmospheric environment including that of Antarctica, giving rise respectively to stratospheric ozone depletion and the Antarctic ozone hole and to global climatic warming, seen at its greatest rate in the region of the Antarctic Peninsula.

To biologists, the Antarctic has always been an important natural laboratory for the study of life under extreme conditions. The terrestrial and limnetic biota may experience drastic environmental contrasts on timescales varying from seasonal to diurnal and spatial scales varying between millimetres and thousands of kilometres - from prolonged darkness in winter to continuous daylight in summer, from a dark and isolated hypolimnion in winter to a stratified lake in summer; from nutrient poor circumstances in isolated nunataks or proglacial lakes to extremely eutrophic situations at the edges of vertebrate colonies and in lakes frequented by seals, from moist subzero circumstances on rock outcrops in the early morning hours, to dry 30°C+ situations later in the day. These environmental circumstances differ profoundly across the Antarctic, which results in significant differences in biogeography in the Antarctic biome.

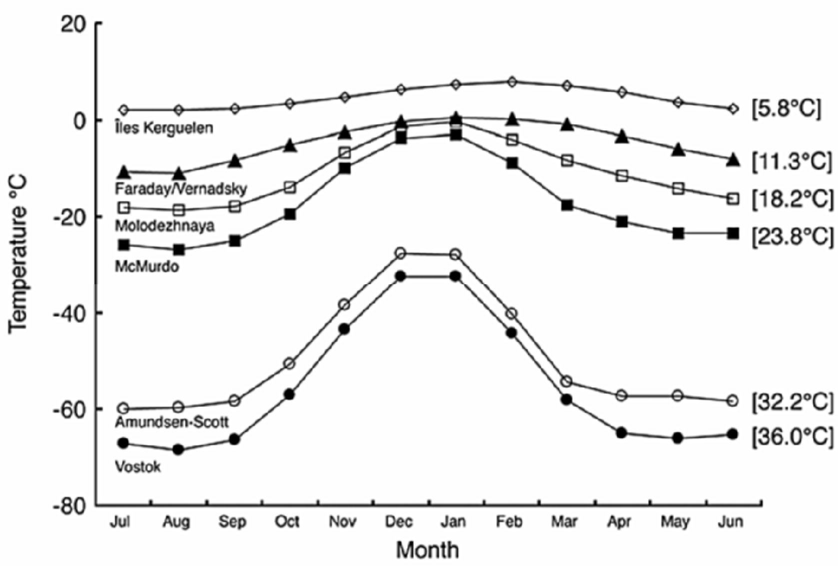

Figure 2. Mean monthly temperatures and annual ranges (°C) at selected Antarctic research stations. Iles Kerguelen represent the subantarctic annual temperature range, Faraday/Vernadsky the maritime Antarctic annual temperature range and remaining stations the continental Antarctic range. There is a clear contrast between the temperature ranges seen at coastal stations in the continental Antarctic (Molodezhnaya and McMurdo) and that of stations on the high plateau (Amundsen-Scott and Vostok) (data from Stonehouse 1989).

Biogeographic zonation

Commonly, three biogeographical zones are distinguished in the Antarctic (Smith 1984), referred to as the subantarctic, the maritime Antarctic and the continental

Antarctic zones (Fig. 1). These zones differ considerably from each other in climatic conditions and, consequently, in species diversity (Smith 1984, Convey 2001b, Chown and Convey this volume, Gibson et al. this volume).

*Table 1. Number of native terrestrial invertebrate taxa reported from the three Antarctic biogeographical zones (updated from Convey 2001b); note that inadequate data are available for many smaller groups, both from a lack of taxonomic knowledge and incomplete survey coverage. * Protozoan taxa for the Subantarctic and maritime Antarctic combined.*

Group	Subantarctic	Maritime Antarctic	Continental Antarctic
Protozoa	83 *		33
Rotifera	>29	>48	13
Tardigrada	>29	24	18
Nematoda	22	29	14
Annelida (Oligochaeta)	23	3	0
Mollusca	5	0	0
Crustacea (terrestrial)	6	0	0
Crustacea (non-marine but including meromictic lakes)	48	11	11
Insecta (total)	210	35	49
Collembola	>92	12	12
Mallophaga	61	25	34
Diptera	44	2	0
Coleoptera	40	0	0
Arachnida (total)	167	36	29
Araneida	20	0	0
Acarina	140	36	29
Myriapoda	3	0	0

The subantarctic zone comprises a series of remote islands and small archipelagos encircling the continent, and includes South Georgia, Marion and Prince Edwards Islands, Iles Crozet, Iles Kerguelen, Heard and McDonald Islands and Macquarie Island. Temperatures in the subantarctic are on average above freezing point year-round (Fig. 2) and precipitation is between 2000 and 3000mm per year (Gremmen 1981). These islands have in common that they are close to or just north of the Antarctic Polar Front (Fig. 1). Large and globally significant populations of seabirds and mammals breed on almost all these islands, contributing significantly to the input of nutrients. With the exception of two duck and one passerine species, indigenous terrestrial vertebrates are not present and the terrestrial fauna consists of invertebrate species (Convey 2001b, Table 1). The subantarctic flora comprises species of nearly all major taxonomic divisions (Stonehouse 1989, Table 2), although is distinctive from that of northern polar and tundra regions through the lack of woody plants and insect-pollinated flowering species.

The maritime Antarctic comprises the western coastal region of the Antarctic Peninsula to about 72°S (Smith 1996), South Shetland, South Orkney and South Sandwich archipelagos and the isolated islands of Bouvetøya and Peter I Øy. The seasonal differences in temperatures experienced are greater than in the subantarctic (Fig. 2), with summer temperatures on average around or slightly above freezing point for two to four months and mean annual precipitation is 400-500mm in the northern maritime Antarctic, decreasing to 50-100mm in the southern Antarctic Peninsula (Walton 1984, Øvstedal and Smith 2001). In summer, there is considerable seasonal snowmelt, which is directly responsible for most liquid water availability in terrestrial ecosystems. Nutrients originate from several sources, including marine vertebrates breeding, moulting or resting on land, transport in melt water, from sea spray aerosols carried inland by wind action and, to a smaller extent, from decomposition of organic material and rock weathering.

Table 2. Number of native plant species in the three biogeographical zones of the Antarctic (after Stonehouse 1989 and Convey 2001b).

Locality	Macrofungi	Lichens	Mosses	Liverworts	Ferns	Angiosperms
Subantarctic	70	>300	250	150	16	56
Maritime Antarctic	30	150	75	25	0	2
Continental Antarctic	0	125	30	1	0	0

Compared to the subantarctic, biodiversity is much reduced. The number of species in the various groups of invertebrates is significantly lower, except for the Protozoa, Rotifera, Nematoda and Tardigrada (Table 1). However, some of these apparent differences are likely merely to reflect the current lack of taxonomic and distributional data available across the Antarctic for these groups, rather than underlying biogeographical features. With respect to the flora, knowledge of species diversity is much more comprehensive (except, perhaps, the macrofungi). Again, species diversity is much lower in the maritime Antarctic - there are only two native angiosperms species (*Deschampsia antarctica* (Poaceae) and *Colobanthus quitensis* (Caryophyllaceae), no ferns and the numbers of lichen, moss, liverwort and macrofungal species are less then 50% of those found in the subantarctic (Table 2). Unlike the isolate island nature of the subantarctic, the maritime Antarctic is an integral element of the Antarctic continent. Although small in area in comparison with the continental Antarctic, it is the region of the continent in which most biodiversity is found.

In terms of area, the continental Antarctic is by far the largest biogeographical zone of the Antarctic biome. It comprises the entire landmass of the continent with the exception of the west coast of the Antarctic Peninsula north of 72°S and the

Balleny Islands. Although the coastal area of the continental Antarctic has a relatively milder climate than the interior of the continent, comparable with that of much of the maritime Antarctic, even in the coastal areas the temperature rarely rises above freezing and then only for short periods with positive mean monthly temperatures experienced for 0-1 months of the year (Walton 1984, Convey 1996a). Annual precipitation is 30-70 mm (Fogg 1998). At inland locations such as exposed nunatak summits and ablation areas such as the Victoria Land Dry Valleys, air temperatures remain permanently and often considerably below zero, while precipitation may be negligible with much of the continental area technically a frigid desert. Nevertheless, microhabitat warming allows liquid water to become available intermittently even in the most southern terrestrial habitats of the Transantarctic Mountains at 84 - 86ºS. The flora and fauna of the continental Antarctic has to be able to function by making use of short and relatively unpredictable windows of opportunity when (microhabitat) temperature are above physiological and biochemical thresholds and moisture becomes available. Only those organisms occur in this zone that are able to withstand prolonged periods of cold and desiccation stress. In the most extreme circumstances, no visible vegetation can be found, with life being limited to endolithic communities of algae, cyanobacteria, fungi, bacteria and lichens that survive in porous rocks such as certain sandstones (Friedmann 1982, 1993).

Key environmental factors

Solar radiation, temperature and moisture availability are key environmental variables governing most processes in terrestrial ecosystems, not least the physiological activity and life history of the individual constituent organisms (Block 1984, Kennedy 1993, Convey 1996b). Together, these physical factors also exert a controlling influence on the release and availability of nutrients. Irradiation may be further modulated by the dynamics of ice and snow cover – the importance of this is clear in limnetic ecosystems (Quesada et al. this volume) but also applies, often on a much smaller physical scale, in the terrestrial environment (Cockell et al. 2002, Arnold et al. 2003). The patterns of variation experienced in these factors, their interactions, optimum levels required in the context of biological activity and the thresholds at which organisms are still able to function are all important determinants of the structure and functioning of the ecosystem as a whole. Temperature (intimately linked with water availability) and solar radiation are the driving forces. Any variation in these factors is likely to have clear and identifiable consequences for Antarctic terrestrial and limnetic ecosystems, with little chance of these being obscured or buffered by the complicated inter-specific relationships existing in the more elaborate ecosystems typical of lower latitudes (Convey this volume).

Isolation

The Antarctic biome has become isolated from biomes at lower latitudes, both because of its obvious geographical isolation from the nearest Southern Hemisphere continents, the existence of the atmospheric Polar Vortex and oceanic Antarctic Polar Front and its history of almost complete glaciation during periods of glacial maxima (Convey 2001a, b, Clarke et al. 2005, Bergstrom et al. this volume). Furthermore, Antarctic terrestrial ecosystems can only be present in areas that are seasonally or permanently snow- and ice-free. These are predominantly present in the coastal zone and at inland nunataks and other oases of exposed ground. These areas, separated on scales of metres to at least hundreds of kilometres by hostile environments of permanent snow, ice or ocean are effectively "islands" of habitat. This isolation has immediate consequences for evolutionary and population processes and genetics, through inducing the isolation of species and populations (Bergstrom et al. this volume, Skotnicki and Selkirk this volume, Stevens and Hogg this volume). Colonisation of newly formed snow- and ice-free areas, once of the most obvious predicted consequences of climate change processes, is dependent largely on the composition of adjacent communities (Hughes et al. this volume, Skotnicki and Selkirk this volume). Moreover, direct human impact on the ecosystems is currently relatively minor, the subantarctic excepted (Frenot et al. 2005, Convey et al. this volume).

Global atmospheric change and the Antarctic climate

The anthropogenic release of chlorofluorocarbons (CFCs) used in various industrial and domestic processes and appliances into the atmosphere, mainly in the Northern Hemisphere, resulted in a decrease in the stratospheric ozone concentration, as CFCs chemically react with ozone under the influence of sunlight. As CFCs concentrate in the atmosphere of the higher latitudes during periods of darkness, a rapid decrease in stratospheric ozone concentration occurs in spring, when the sun comes above the horizon again. The resulting 'ozone hole' was first described by Farman et al. (1985). Since then, in most years the Antarctic ozone hole has become 'deeper' (more depleted), wider and more prolonged, and any improvements consequential on the adoption of the internationally agreed Montreal Protocol aimed at reducing CFC emissions have yet to become apparent. The biological consequences of ozone depletion, to which the Antarctic is specifically exposed through the general position of the ozone hole being determined by atmospheric circulation processes, are described by Hennion et al. (this volume).

Since the start of modern industrialisation in the Northern Hemisphere in the 19th Century, large amounts of infrared-absorbing gases have been released into the atmosphere. These so-called greenhouse gases have induced a general increase in mean annual atmospheric temperatures, and subsequently in the annual mean surface temperatures and most recently in sea temperatures. The present view is that a global mean temperature increase of approximately 2°C and attendant changes in precipitation regimes, are realistic expectations over the next 50 years (IPCC 2001). Moreover, because large-scale extinctions and movements of species ranges are known to have resulted from major climate changes in the past (Coope 1995, Roy et al. 1996), an ability to predict the consequences to biodiversity of climate change is becoming increasingly important (Mc Neeley et al. 1995).

Over the last 50 years, air temperatures and moisture regimes in parts of the Antarctic have changed markedly (Frenot et al. 1997 Weller 1998, Smith et al. 1996, King and Harangozo 1998, King et al. 2003, Convey this volume), with most recently parallel changes in near-surface sea temperatures being reported (Meredith and King 2005), and the indications are that these trends will continue. This increase is especially apparent in the Antarctic Peninsula region, where summer temperatures have increased since the 1950s by about 2°C and winter temperatures by about 5°C (King et al. 2003). However, in other areas of the Antarctic, temperature increases have been much lower and some areas have recorded regional cooling (Turner et al. 2005).

Invasive species

Human trade and movement across the planet have led to accidental or deliberate transport and introductions of virtually all groups of biota. Until the last two centuries or so, Antarctica's isolation has protected it from such invasions, but this protection has been rapidly overcome, particularly in the Subantarctic (Frenot et al. 2005, Convey et al. this volume). Here, deliberate introductions of vertebrates include reindeer, cattle, sheep, cats and rabbits, while rats and mice were introduced inadvertently. Such introductions have a profound influence on the native biota (eg Vogel et al. 1984, Chapuis et al. 1994, Smith 1996, Chown and Block 1997, Chown et al. 1998). A range of plant species have been introduced both deliberately and inadvertently to almost every subantarctic island, while many reports also exist on the introduction of invertebrate species (Frenot et al. 2005, Convey et al. this volume). About half of the recorded vascular flora of South Georgia comprises plant species introduced from South America and Europe (Convey 2001a), with some of these displacing the native flora (Smith 1996). On Marion Island, the native flora is out-competed by invasive species such as *Agrostis stolonifera* (Gremmen 1997, Gremmen and Smith 1999, Convey et al. this volume). However, establishment of alien species to the maritime Antarctic are few to date, including a dipteran and an enchytraeid worm known to have been introduced to Signy Island (Convey and Block 1996) and the grass *Poa pratensis* to the northern Antarctic Peninsula (Smith 1996, Convey et al. this volume).

While introductions are not of necessity directly connected with climate change, any increase in temperature, especially in connection with an increase in water availability, may both lower the barriers to the long distance transport stage of the colonisation process and provide opportunities for invading species to establish after arrival and survive better the adverse season, allowing them subsequently to expand at the expense of the native fauna and flora (Bergstrom and Chown 1999, Frenot et al. 2005). Increased human activity and freedom to travel separately further lowers these barriers, through bypassing the need for survival of long distance atmospheric or oceanic transport.

Responses of the biota

In many areas of the Antarctic, the biota has already shown pronounced direct and indirect responses to both climate change and the invasions of alien species (Chown and Smith 1993, Fowbert and Smith 1994, Kennedy 1995, Ellis-Evans et al. 1997, Frenot et al. 2005). Currently processes in both terrestrial (Convey this volume) and in limnetic ecosystems (Lyons et al. this volume) and the links between the two (Quesada et al. this volume) are being studied by many groups of Antarctic ecologists.

Custodians

Humanity's role in the Antarctic has changed since the early explorers' visits to the region, progressing from that of an explorer and hunter to that of an investigator and, increasingly, as a custodian. Uniquely on the planet, people's activities in Antarctica are governed by international agreements under the Antarctic Treaty System. Within this System, many regulations have been agreed by the various member states over the last decades, amongst which are clear recognition of the fragility of the Antarctic and stipulation on the need and means for protection. Understanding the effects of climate change on the Antarctic environment has fundamental implications for the way in which we protect this environment (Whinam et al. this volume, Hull and Bergstrom this volume). Our increasing knowledge of the region and its biome only serves to emphasise that this exceptional environment must be treated with care, not only as part of our legacy for future generations but also because the Antarctic is intricately linked with, and plays a fundamental role in, global processes and, hence, the environment we ourselves inhabit.

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2. THE PHYSICAL SETTING OF THE ANTARCTIC

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Introduction

DEFINITION OF AREA COVERED BY THIS BOOK

The Antarctic terrestrial and freshwater biome examined here includes the main continental landmass, the maritime Antarctic including the Antarctic Peninsula and associated islands and archipelagos (South Shetland, South Orkney, South Sandwich Islands, Bouvetøya) and the subantarctic islands which lie on or about the Antarctic Polar Frontal Zone (PFZ), an oceanic and climate boundary where the Antarctic Circumpolar Current (ACC) meets warmer waters. These geographic regions are also meaningful biogeographical regions (see discussions in Skottsberg 1904,

D.M. Bergstrom et al. (eds.), Trends in Antarctic Terrestrial and Limnetic Ecosystems, 15–33.

Pickard and Seppelt 1984, Smith 1984, Longton 1988, Chown and Convey this volume, and see Fig. 1 in Huiskes et al. this volume), if still under refinement (Peat et al. in press) and provide useful platforms for the discussions below. The purpose of this chapter is to briefly review the environmental factors, both past and present, that are or have been evolutionary forcing variables influencing the development of the present-day biological diversity of Antarctica.

THE FORMATION OF THE ANTARCTIC CONTINENT

A sensible place to begin an examination of the influence of the physical environment on past biodiversity is some 100 million years ago (MA) when Antarctica was part of the supercontinent Gondwana and the subantarctic islands were non existent. During the early Cenozoic (>100-60MA), Gondwana began to fragment and the first major oceanic barriers to the movement of terrestrial species were formed (McLoughlin 2001). Antarctica, one of the elements of the former Gondwana supercontinent, drifted over the southern polar region. The continent's high latitude location, inevitably linked with seasonal periods of complete darkness, did not immediately lead to massive extinction of terrestrial fauna and flora, which remained typical of south–temperate rainforest regions for a long period subsequently (Feldmann and Woodburne 1988, Clarke and Crame 1989, Poole and Cantrill 2001, Francis and Poole 2002). Even after the commencement of ice sheet formation, the Antarctic experienced periods when this biota could show local expansion, until as recently as 8-10MA.

In the early Miocene, Antarctica finally became fully isolated from the Gondwana supercontinent with the full opening and deepening of the Drake Passage (28-23MA) and the separation of the Tasman Rise from Antarctica (33.5MA) (Livermore et al. 2005, Scher and Martin 2006). These tectonic processes resulted not only in the elimination of the last land-bridge connections with lower and more temperate latitudes but also in the onset of the deep-water circulation around the Antarctic continent of the Antarctic Circumpolar Current (ACC). The ACC eventually resulted in the isolation of a cool body of water (the Southern Ocean) and the establishment of the Polar Frontal Zone (PFZ). This PFZ further isolated Antarctica, its outlying archipelagos and the Southern Ocean from other continents and oceans, climatically, thermally and oceanographically and set the stage for the development of distinct Antarctic biological communities adapted for survival in the southern polar region (Barnes et al. 2006).

These movements of the Antarctic continental plate were associated with many periods of volcanism. The plate is encircled by divergent plate boundaries along roughly 95% of its perimeter and is broken internally by numerous rift-structures suggesting a plate-wide extensional tectonic regime. Within this environment, the Antarctic Plate evolved into one of the great alkaline volcanic provinces of the world (LeMasurier and Thompson 1990). Volcanism has been and continues to be involved in the formation of the many of the subantarctic and Antarctic islands. Some of these consist of volcanic rocks overlying continental basement rocks, such as the convergent plate margin volcanoes of the South Sandwich Islands. Iles Kerguelen and the Heard and McDonald Islands which, although they specifically have lacustrine bases, are part of the mostly underwater Kerguelen Plateau, which contains Gondwana fragments overlain by more recent volcanic rocks (Gladczenko and Coffin 2001). Marion and Prince Edward Islands and Iles Crozet are shield volcanoes, erupting 0.11-0.21MA and 0.2-9MA (LeMasurier and Thomson 1990).

South Georgia however, contains continental elements whilst Macquarie Island is the aerial portion of a ophiolite complex, a piece of largely intact seafloor at the junction of the Australasian and Pacific tectonic plates, emerging from the sea approximately 0.6MA (Adamson et al. 1995). The Antipodes, Auckland and Campbell Islands lie on the Campbell Plateau, underlain by continental crust that was part of Antarctica in pre-Cenozoic time (McLoughlin 2001).

The majority of subantarctic and Antarctic islands are substantially younger than the Antarctic continent with the oldest, Iles Kerguelen, only 39MA. There are at least 16 Antarctic and subantarctic volcanoes that are known to be active (including subantarctic Heard Island, most of the maritime Antarctic South Sandwich Islands, Deception Island and Bouvetøya, and Mounts Erebus, Melbourne and Rittman in continental Antarctic Victoria Land) and a further 32 suspected of Holocene activity (LeMasurier and Thompson 1990, Convey et al. 2000a, Fitch et al. 2001, Anon 2005).

The continental ice sheet

The Earth was in a state of extreme global warmth from the Cretaceous (144-65MA) to the early Eocene (c. 55MA). However, by the middle to late Eocene (42MA), there were a series of several small glaciations and one major transient glaciation of the Antarctic continent. These abrupt climate reversals were possibly associated with the first opening of the Drake Passage at 41MA (Scher and Martin 2006). Studies of the oxygen isotope composition of marine calcite suggest that the greenhouse to icehouse transition was closely coupled to the evolution of atmospheric carbon dioxide, and that negative carbon cycle feedbacks may have initially prevented the permanent establishment of large ice sheets (Tripati et al. 2005). However, by 34MA, at the Eocene-Oligocene transition, large ice sheets appeared on the Antarctic continent, evidenced by decreasing atmospheric carbon dioxide concentrations and a deepening of the calcite compensation depth in the world's oceans, coinciding with changes in seawater oxygen isotope ratios (glaciation in the Northern Hemisphere began much later, between 10 and 6MA). There are two theories why the ice sheet formed at this time. The first, involves the separation of Antarctica from the Australian and South American continents and the opening of the ocean gateways that allowed the establishment of the east to west flow of the circumpolar currents in the Southern Ocean (Kennett 1977). This led to the thermal isolation of the continent, cooling and the formation of sea ice and the continental ice sheet. The second theory puts more emphasis on the role of global atmospheric CO_2, orbital forcing and ice-climate feedbacks, with the opening of the Southern Ocean gateways playing a secondary role (DeConto and Pollard 2003). The rapid decrease in CO_2 at about 34MA brought with it a decrease in temperature sufficient for viable snow and ice to remain present throughout the year. After 15MA, a further cooling is believed to have caused the transition from an ephemeral to a permanent Antarctic ice sheet (Barret 2003). However, since its formation, this ice sheet has been far from stable and over time has exerted strong physical controls on where biological communities have survived and hence underpins many of the biogeographical patterns seen today.

During the most recent geological period, the Quaternary, that spans approximately the last 2MA, the polar ice sheets developed their characteristic cycle of slow build up to full glacial conditions, followed by rapid ice melting and deglaciation to interglacial conditions (Williams et al. 1998). These frequent changes in the configuration of the ice sheets have been driven by the cyclical changes in the Earth's orbital path around the sun (Milankovitch cycles). The most influential of these are the 41kyr (thousand years) obliquity cycle and the 100kyr eccentricity cycle (Williams et al. 1998). The continuous cycles of expansion and contraction of the east and west Antarctic ice sheets has resulted in the regular displacement of the terrestrial and freshwater environments suitable for survival or successful colonisation and establishment of biota.

What is most remarkable about the Quaternary history of Antarctica is that the periods of greatest habitat availability, the interglacials, have been relatively short-lived and unusual. The ice core record from Dome C shows that, in the period from for 430-740kyr BP when climate variability was dominated by the 41kyr obliquity cycle, the Antarctic has been c. 50% in the interglacial phase, although these were weaker interglacials than experienced at present. However, in the last 430kyr BP, when climate variability has been dominated by the 100kyr Milankovitch eccentricity cycle, the Antarctic has been c. 90% in the glacial phase (EPICA 2004) and some cold periods have been sustained for more than 60kyr (eg 140-200kyr: Jouzel et al. 1993). Thus, with only c. 10% of the late Quaternary being in full interglacial conditions, for most of this time displacement and retreat of the Antarctic biota, either to refugia or possibly to lower latitudes, appears to be the norm. However, there are some examples of parts of some Antarctic oases remaining ice free through the Last Glacial Maximum (LGM) (18-22kyr) based on evidence contained in lake sediments and other terrestrial deposits (Hodgson et al. 2001, Hodgson et al. 2005, Cromer et al. in press) and some areas such as the Prince Charles mountains have been ice-free for possibly millions of years (Fink et al. 2000). Similarly, some nunataks, which remained above the altitudinal limit of the

LGM ice sheet, contain evidence of a refuge fauna (Marshall and Pugh 1996, Marshall and Coetzee 2000, Convey and McInnes 2005) that may have subsequently been available to recolonise surrounding areas after the ice retreated and suitable habitats became available.

Despite these refugia, a result of the glaciological history of Antarctica is that the majority of the continental high-latitude habitats are likely to have formed in the present, Holocene, interglacial whilst the maritime Antarctic and some warmer subantarctic islands are likely to have had longer periods of exposure, at least in some areas. For example, the consistently low elevation of Macquarie Island, since its emergence 600 000 years ago has meant that glaciation has played a minor role in shaping the island's landscape (Selkirk *et al.* 1990, Adamson *et al.* 1995). However, along the Antarctic Peninsula and associated archipelagos, and the linked Scotia arc subantarctic island of South Georgia, there remains an apparent contradiction between ice sheet and glaciological reconstructions at LGM, which require considerable expansion in ice depth and extent (the latter to the continental shelf edge) with implicit obliteration of all low altitude terrestrial habitats, and increasing biological evidence in support of an ancient and vicariant indigenous terrestrial biota (Clapperton and Sugden 1982, 1988, Larter and Vanneste 1995, O Cofaigh *et al.* 2002, Convey this volume, Chown and Convey this volume).

A schematic model of Antarctic biodiversity

Present-day biodiversity in the Antarctic is the result of a number of factors that can be summarised in a simple schematic model (Fig. 1). The main elements of biodiversity are the continued existence of past biota, the presence or creation of habitat suitable for colonisation, the arrival and establishment of new colonisers, and the adaptation and selection of new taxa in response to environmental forcing variables associated with environmental change.

The expansion and contraction of the Antarctic ice sheet has undoubtedly led to the local extinction of biological communities on the Antarctic continent during glacial periods (Hodgson et al. 2006). Subsequent re-colonisation and the resulting present-day biodiversity is then a result of whether the species were vicariant (surviving the glacial maxima in refugia, then recolonising deglaciated areas), arrived through post-glacial dispersal from lower latitude islands and continents that remained ice free (Pugh et al. 2002), or are present through a combination of both mechanisms. Evidence can be found to support both vicariance (Marshall and Pugh 1996, Marshall and Coetzee 2000, Stevens and Hogg 2003 this volume, Allegrucci et al. 2005, Cromer et al. in press) and dispersal (Hodgson et al. 2006) for a variety of different species, and is based on the level of cosmopolitanism (dispersal model) or endemism (vicariance model) (Gibson et al. this volume), on direct palaeolimnological evidence or, most recently, on molecular phylogenetic and