

2. THE PHYSICAL SETTING OF THE ANTARCTIC

D. M. BERGSTROM

*Department of Environment and Heritage
Australian Government Antarctic Division
203 Channel Highway
Kingston, Tasmania 7050, Australia
dana.bergstrom@agad.gov.au*

D.A. HODGSON

*British Antarctic Survey, Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET, United Kingdom
daho@bas.ac.uk*

P. CONVEY

*British Antarctic Survey, Natural Environment Research Council
High Cross, Madingley Road
Cambridge CB3 0ET, United Kingdom
p.convey@bas.ac.uk*

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,

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 (Tripathi 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 CO₂, 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 CO₂ 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

evolutionary studies (Skotniki and Selkirk this volume, Stevens and Hogg this volume).

On the oceanic islands, the biotas will have originally arrived via long-distance over ocean dispersal, with vicariance and dispersal playing subsequent roles in shaping the biodiversity across glacial cycles (Marshall and Convey 2004). Species on Southern Ocean islands show conventional island biogeographic relationships, with variance in indigenous species richness explained by factors including area, mean surface air temperature, and age and distance from continental land masses (Chown et al. 1998). For aquatic species, at least some groups such as the diatoms, diversity is controlled by the ‘connectivity’ among habitats with the more isolated regions developing greater degrees of endemism (W. Vyverman pers. comm.).

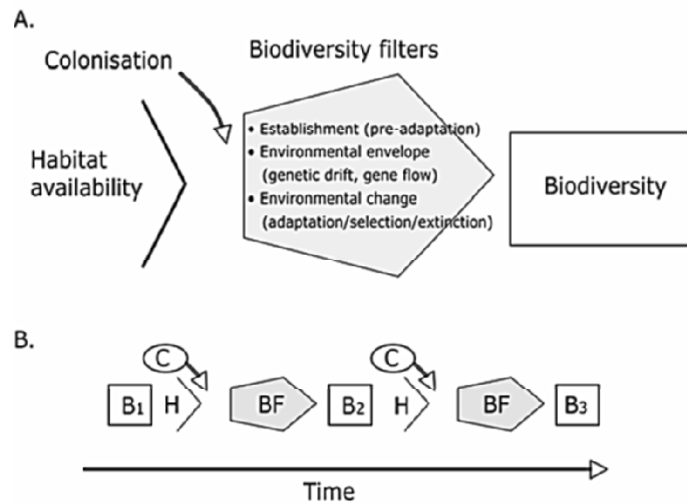


Figure 1. Schematic model illustrating factors influencing the formation of the biodiversity in a location at one time (A.), and how this changes with the passing of time and associated climate change (B).

PAST BIODIVERSITY

As described above, there is some evidence for the survival of biodiversity on the Antarctic continent and subantarctic islands through the LGM. Some taxa are recognised as Antarctic endemics. In the near future, the use of modern genomic tools will provide greater insight into the proportion of the current biota that are glacial survivors, either original species or vicariant derivatives and for what length of time these organisms have been present in these landscapes (Peck et al. 2005).

HABITAT AVAILABILITY

The first requirement of establishment is that there needs to be a substrate and habitat on and within which it is possible for colonisers to become successfully established. The main habitats for terrestrial life in Antarctica include ice-free areas of the islands and continent and inland nunataks that are surrounded by ice. Combined, these ice-free areas account for only 0.35% of the Antarctic continental area (Fox and Cooper 1994). On subantarctic islands, ice-free areas range from small coastal pockets interspersed with glaciers (South Georgia and Heard Island) to completely ice-free islands such as Macquarie and the Iles Crozet. Water bodies range from small holes in the ice (cryconites) to ponds and very large freshwater or saline lakes (Gibson et al. this volume and Quesada et al. this volume). Wet seepage areas are also present in many ice free regions. Adjacent to coasts lakes can be formed either by isolation of basins from the sea during postglacial isostatic rebound, or proglacially as glaciers and ice sheets retreat on the land (Hodgson et al. 2004, Lyons et al. this volume, Quesada et al. this volume). The majority of these habitats are Holocene in age (last 11 ka). However, some areas have survived glaciation due to their altitude or glaciological settings. Examples of at least parts of some Antarctic oases remaining ice free through the Last Glacial Maximum include the Larsemann Hills (Hodgson et al. 2001), the Schirmacher Oasis (Schwab, 1998) and possibly the Bunger Hills (Gore et al. 2001) based on evidence contained in lake sediments and other terrestrial deposits. Similarly, some nunataks have remained ice free through a number of glacial cycles. Subglacial lakes have also likely been present in some form for many millennia (Doran et al. 2004), but are outside the scope of this volume.

COLONISATION

Colonisers are carried in the air, on visiting birds and mammals (including humans) or sometimes borne on rafts (logs, kelp rafts) on the surface of the ocean (Hughes et al. this volume). The terrestrial environments of the Antarctic have been in a fairly constant if low level state of invasion and reinvasion from temperate and closer regions (Barnes et al. 2006) and are currently facing a considerable increase in invasion pressure through the direct (deliberate and accidental transport) and indirect (climate change acting to reduce the hurdles required for either successful natural long distance transport or establishment) (Frenot et al. 2005a, Convey et al. this volume b). For example, two vascular plant species on Macquarie and a further two on Heard Island have been identified as having colonised and established only in the last 200 years, with one of Heard Island species (*Leptinella plumosa*) being represented by only one plant found in 2003 (Bergstrom et al. in press, Turner et al. 2006). In recent decades, new populations of the hair grass *Deschampsia antarctica* and small cushion plant *Colobanthus quitensis* have been appearing in various

locations on the Antarctic Peninsula (Fowbert and Smith 1994, Grobe et al. 1997, and review by Convey 2003).

Table 1. Present-day distribution and colonisation attributes of Antarctic biota in the subantarctic, maritime and continental Antarctic biogeographic zones (S, M, C, respectively).

Group/taxon	Distribution S, M, C	Colonization diaspora	Major dispersal methods
Mites	S,M,C	none	self-propulsion, zoochory
Insects	S,M	adults	aerial, zoochory
Nematodes	S,M,C	eggs, anhydrobiotic stages	aerial, zoochory
Collembola	S,M,C	active juveniles and adults	aerial or water surface
Crustaceans	S,M,C	adult resting stages (some groups), resistant eggs	aerial or water
Tardigrades	S,M,C	eggs, resistant adult state (tun)	aerial, zoochory
Molluscs	S	eggs	water
Testate amoeba	S,M,C	resistant stages	aerial or water
Spiders	S	adults and young	aerial
Annelids	S,M	juveniles and adults	water
Angiosperms	S,M	seeds, fruits	aerial or water, birds
Ferns	S	spores	aerial
Mosses	S,M,C	spores, plant fragments	aerial, birds
Algae	S,M,C	spores	aerial or water, birds
Lichens	S,M,C	spores and other propagules, fragments	aerial, birds
Freshwater phytoplankton	S,M,C	spores and fragments	aerial, birds
Bacteria	S,M,C	spores	aerial, birds
Cyanobacteria	S,M,C	cysts, fragments	aerial, birds
Yeasts	S,M,C	spores	aerial
Macrofungi	S,M	spores	aerial, birds
Microfungi, mycorrhizae	S,M,C	spores	aerial

Some groups of organisms are better adapted to dispersal (Table 1) and this determines the frequency with which they arrive at new habitats, but not their ability to establish there. Other organisms have limited motility but have established and survived in various refugia on account of their ability to withstand a series of selective pressures. In an examination of patterns in biogeography of Southern Ocean Islands, Greve et al. (2005) identified the level of vagility within biotic groups as an important characteristic, with more vagile taxa supporting the hypothesis of single origins of Southern Ocean biota, while those less vagile supporting a multi-regional scenarios. In a separate analysis, Muñoz et al. (2004) identified an over-riding influence of wind dispersal as an explanatory factor underlying biogeographical patterns seen across the subantarctic islands.

ESTABLISHMENT (PRE-ADAPTATION)

Once colonising organisms are present they are subjected to a variety of selection pressures or biodiversity filters either before they become established or after. Organisms that establish after colonisation in the Antarctic are, by evidence of their successful establishment event, pre-adapted to the local conditions, either through a particular character state or being phenotypically plastic. This is not to say that such organisms are operating optimally – indeed optimality is an erroneous assumption often applied even to indigenous Antarctic biota with no real evidence - and ecophysiological studies of Antarctic organisms have demonstrated for example, that optimal temperatures for particular processes or activities are often well above ambient Antarctic or subantarctic air or water temperatures (Convey 1996, Hennion et al. this volume). The continued persistence of biota operating under sub-optimal conditions is further encouraged by the generally low importance of negative biotic factors (ie competition, predation) relative to abiotic environmental variables in such habitats (Convey 1996). The survival threshold can be understood as the achievement, over time, of a net gain in carbon and biomass, allowing viability to be maintained and some form of reproduction (requisite for the long-term development of a viable population) to occur. Failure to reach an effective population size will ultimately lead to extinction and, indeed, it is likely that many initially successful establishment events do not go on to establish populations of the species concerned. Convey et al. (2000b) suggested that evidence for such a pattern of frequent dispersal and extinction could be seen in interpreting differences in biodiversity associated with geothermally-influenced ground found in two surveys of the maritime Antarctic South Sandwich Islands separated by ~ 30y.

ENVIRONMENTAL ENVELOPE (GENETIC DRIFT, GENE FLOW)

Descriptions of environmental conditions and features found in Antarctic and subantarctic environments are available from a number of sources (Walton 1984,

Selkirk et al. 1990, Kennedy 1993, Convey 1996, Bargagli 2005). The most prominent environmental drivers in terrestrial environments are photoperiod (varying with the degree of latitude south), the period temperatures are above zero, the upper and lower limits of the thermal range and the, related, availability of free water. In order to sustain ecosystems based on carbon fixation by terrestrial autotrophs, conditions must allow for summer carbon storage to be greater than year-round respiratory loss and for selection of adaptations for a resting stage or dormancy. In limnetic environments, key features again include the availability of free water in addition to the degree of salinity, depth, nutrient availability and the longevity and depth of surface ice, although the selection of mixotrophy (Gibson et al. this volume) reduces the reliance on carbon fixation by autotrophic processes. The degree of temperature fluctuation is dependant on the depth of the water body. As in other environments, stochastic events also play a major role (see below), particularly with regard to local extinction. For example, satellite imagery of volcanic McDonald Island suggests that most vegetation has been destroyed with recent substantial volcanic activity, while the geothermal plant and animal communities associated with active fumaroles described from the South Sandwich Islands and Deception Island (Convey et al. 2000a, Smith 2005) are temporally defined by the geologically ephemeral persistence of specific individual habitats.

After establishment, changes to the genetic population structure can occur through population processes such as genetic drift and gene flow. Some moss populations in continental Antarctica, have been found to have had as much genetic variation as temperate populations, while others are extremely limited (Skotknicki and Selkirk this volume). As mosses in the continental Antarctica are not known to undergo sexual reproduction to any significant extent (Smith and Convey 2002), genetic variation can be attributed to mutation, genetic drift or multiple colonisation events. Over the longer term (million year timescale) molecular phylogenetic studies of differentiation within Victoria Land springtails have been used to propose the existence of, and expansion from, refugia (Stevens and Hogg 2003, this volume), and the allopatric differentiation of populations isolated by glacial advances followed by contact being re-established (Nolan et al. in press). Over an even longer timescale of tens of millions of years, a molecular clock approach applied to species of Diptera endemic to the Antarctic Peninsula and subantarctic South Georgia has proposed separation events carrying a signal of the geological separation of the different tectonic elements linking this region with southern South America (Allegrucci et al. 2006).

ENVIRONMENTAL CHANGE (ADAPTATION/SELECTION EXTINCTION)

The key processes of adaptation, selection and extinction are inevitably linked with environmental change. The gross extinctions of Tertiary ecosystems across the Antarctic and Iles Kerguelen and Heard Island (McLoughlin 2001 and Truswell et

al. 2005) are major examples of the impact of climate change on ecosystems. Extinctions associated with cooling (eg leading up to the LGM and previous events) would have been reflected both in species loss due to environmental conditions shifting below their climatic envelope in addition to the loss of habitat from ice advance.

Species that had colonised the region pre-Tertiary and survived glaciations in refugia, may have been pre-adapted with sufficiently plasticity to cope with the environmental changes to be experienced, or have evolved *in situ* in response to the selection pressures of changed environmental conditions. The break-up of Gondwana, the creation of islands and loss of habitat through ice advance isolated many environments, thus the role of genetic drift and mutations most likely played a greater role in populations, both in terrestrial and freshwater environments, than gene flow.

Although, as already mentioned, Antarctic biota are not necessarily functioning under optimal conditions, many species display both southerly and northerly limits to their distribution within the region. Fig. 2 illustrates the distribution of *Acaena magellanica*. This species, producing fruits with four barbed spines that are dispersed as an aggregate containing hundreds of fruits, is highly vagile. Thus, its distribution pattern is not limited by dispersal capacity and illustrates a degree of physiological tolerance. Balls of fruits are often seen caught on the bodies of migratory birds such as the Brown Skua and are readily transported accidentally by humans caught on clothing (Whinam et al. 2004). The southern distributional limit of *A. magellanica* is on South Georgia and the warmer (eastern) side of Heard Island, while the species has not been found in Tasmania, New Zealand or on New Zealand's southern islands. It seems highly unlikely that propagules of such a highly vagile species have not dispersed to these warmer localities where other members of the genus occur. This is an example of a species whose life history strategies have been selected for survival under cooler subantarctic environmental conditions (Convey et al. this volume a).

While climate change research is heavily focussed on the identification of large scale trends, the role of extreme and/or local events under environmental change must not be overlooked. Fig. 3 illustrates that in biological systems it is extreme events that can have the most impact in a local population, be it under a more general cooling or warming environment. Such extreme events, that exceed the physiological thresholds of a species, can lead to local extinction despite the general trend in environmental change occurring within the operating climatic envelope of the species.

The 2001/02 austral summer may provide a recent example of such an extreme event: in this season air temperatures exceeding 10°C were recorded in the Ross Sea region, flooding occurred in the Dry Valleys from melting glaciers and rain occurred at the coastal continental Dumont D'Urville station (Lyons et al. this volume, Wall in press, D. Bergstrom, E. Woehler and M. Pook unpubl. data). This was despite

analyses identifying a general decadal-long cooling trend in this region (Doran et al. 2002). Increased free water associated with rain can increase opportunities for population growth and expansion, however increased temperatures without accompanied free-water can lead to increased stress from drought in terrestrial environments (Convey 2003, this volume) or increased salinity in freshwater environments.

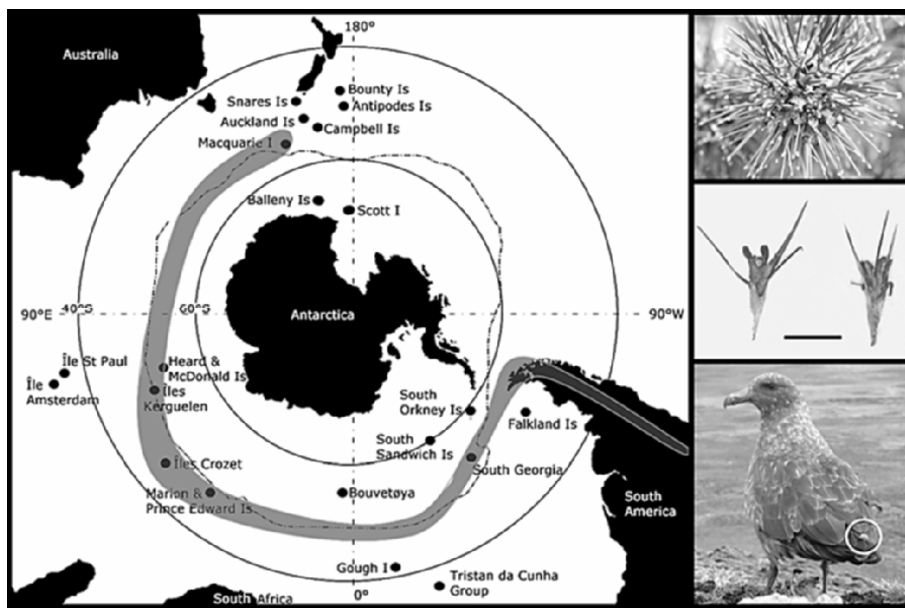


Figure 2. A map of the current distribution of the subantarctic herb *Acaena magellanica*. The three figures illustrate an *Acaena* fruit head showing abundant spines (top), two fruits - the scale bar is 3mm (middle) and an *Acaena* fruit head on a subantarctic skua. Photographs by K. Kiefer.

Biotic interactions (enhancement/inhibition/extinction)

Species richness can be exceedingly low in some Antarctic environments, but species generally do not exist alone. The simplest soil faunal communities on the planet are found in Antarctica, with those of the Victoria Land Dry Valleys being restricted to nematodes, tardigrades, rotifers and protozoan groups (Freckman and Virginia 1997), and those of inland Ellsworth Land nunataks losing even the nematodes (Convey and McInnes 2005). Even these extremely simple communities contain autotrophic, consumer and predatory trophic levels. Therefore, the species involved are subjected to a range of interactions with other species, ranging through

mutually beneficial, neutral and negative impacts from competition, predation and parasitism. Bergstrom and Chown (1999), however, have also noted that on Southern Ocean islands many functional groups were missing from communities, a trend that is thought to be even more exaggerated in more southerly and less complex ecosystems. Thus the range of interactions is thought to be reduced compared with warmer ecosystems and, as already stated, biotic factors are thought to become relatively unimportant as evolutionary selective pressures.

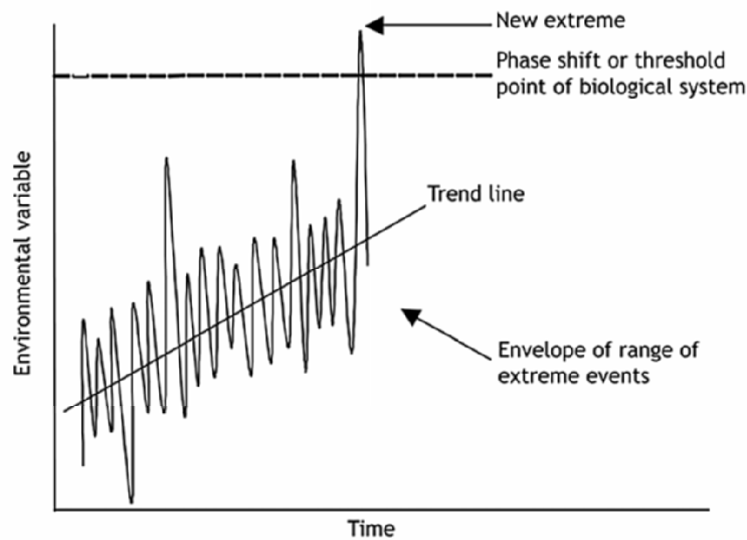


Figure 3. Schematic illustrating the potential importance of extreme climatic events even during a period of apparently ameliorating climatic regimes.

In the subantarctic, there are some indications of the impact of competition. The cushion plant species *Azorella selago* and *A. macquariensis* are limited primarily to higher altitude locations on their respective subantarctic islands, ascribed to the low capacity of these species to cope with competition from taller plants (Bergstrom and Selkirk 2000). It is often the case that introductions of non-indigenous species bring stronger competitors into communities – for instance, the introduction of a predatory carabid beetle to lowland terrestrial habitats of South Georgia and Kerguelen has had clear and considerable impacts on other indigenous invertebrate species (Ernsting et al. 1995, Chevrier et al. 1997, see reviews by Frenot et al. 2005a, Convey et al. this volume b).

Examples of positive biotic interactions include the presence of mycorrhizae in the tissues of plants, including liverworts in Antarctica and the roots of many subantarctic vascular plants (Williams et al. 1994, Laursen et al. 1997, Frenot et al. 2005b, K. Newsham and R. Upson, unpubl. data). Mycorrhizae have been identified

as playing an important role in nutrient uptake by plants, and widespread observations across many environments support the idea that they can influence the colonisation capacity of plants in cold and low-nutrient environments such as subantarctic glacier forelands (Frenot et al. 2005b).

An interesting and unforeseen negative biotic interaction is currently occurring on some sub- and maritime Antarctic islands. Over the last two decades, populations of fur seals have been expanding at a substantial rate, following their virtual extermination, and that of the great whales, by humans during the 19th and early 20th Centuries (Hodgson and Johnston 1997). As a result, terrestrial habitats occupied by seals during their breeding and moulting seasons are increasing. This is leading to extensive vegetation destruction and excessive manuring, of local vegetation communities, particularly in the South Shetland and South Orkney Islands and on South Georgia and Heard Islands, and to rapid eutrophication of previously oligotrophic limnetic ecosystems (Smith 1988, Butler 1999).

Summary

Present-day Antarctic biodiversity is an inventory of the species present at one time, while the factors that control biodiversity are operating more or less continuously and at a variety of different scales. Thus, determining which species survive and evolve in the Antarctic region, and for that matter in any environment, is dependent on many factors.

Antarctica and its surrounding islands have undergone significant evolution of their landscapes and climate over the last 60 MA. The same biological processes (habitat availability → colonisation → biodiversity filters → resultant biodiversity) that occur elsewhere on the planet operate in both limnetic and terrestrial ecosystems in ice-free refugia in Antarctic and peri-antarctic islands, but the impact of some processes or environmental stressors is greater than in other localities. Currently, what separates the Antarctic from other ecosystems in the world is the combination of extremes that it experiences: extreme isolation, extreme past loss of habitat from ice formation and extreme selection pressure particularly from temperature and water stress in the terrestrial environment.

What we see as a result of these factors at a continental scale is drastically reduced biodiversity at the species level. We now have a situation where many species are at their distributional limits, both northern and southern, and the environment in many places is changing rapidly and thus selection leading towards future biodiversity is most acute. Convey (this volume) and Lyons et al. (this volume) expand on evidence for recent change and discuss the future under current climate change scenarios.

With a long, complex and extreme history, Antarctica and its surrounding islands currently provide relatively simple natural laboratories where small changes impact

greatly and this impact is perceivable by the human observer. Apart from its obvious but value-based attributes such as wilderness, aesthetic and existence values, this one attribute makes the region a precious asset to the human race.

References

- Adamson, D.A., Selkirk, P.M., Price, D.M. and Ward, N. (1995) Uplift of the Macquarie Ridge at Macquarie Island: Pleistocene evidence from raised beaches and topography. *Climate Succession and Glacial History of the Southern Hemisphere over the Past Five Million Years. ANARE Research Notes* **94**, 3-5.
- Allegretti, G., Carchini, G., Todisco, V., Convey, P. and Sbordoni, V. (2006) A molecular phylogeny of Antarctic Chironomidae and its implications for biogeographical history, *Polar Biology*, **29**, 320-326.
- Anonymous (2005) Recent volcanic activity at McDonald Island, <http://www.heardisland.aq>
- Bargagli, R. (2005) Antarctic ecosystems: environmental contamination, climate change, and human impact. *Ecological Studies* Vol. 175, 395 pp. Springer, Berlin.
- Barnes, D.K.A., Hodgson, D.A., Convey, P., Allen, C.S. and Clarke, A. (2006) Incursion and excursion of Antarctic biota: past, present and future, *Global Ecology and Biogeography*, **15**, 121-142.
- Barrett, P.J. (2003) Cooling a continent. *Nature*, **421**, 221-223.
- Bergstrom, D.M. and Chown, S.L (1999) Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology and Evolution*, **14**, 472-477.
- Bergstrom, D.M. and Selkirk, P.M. (2000) Terrestrial vegetation and environments on Heard Island. *Papers and Proceedings of the Royal Society of Tasmania*, **133**, 33-46.
- Bergstrom, D.M., Turner, P.A.M., Scott, J.J. Copson G. and Shaw J. (in press) Restricted plant species on subantarctic Macquarie and Heard Islands. *Polar Biology*, DOI 10.1007/s00300-005-0085-2.
- Butler, H.G. (1999) Seasonal dynamics of the planktonic microbial community in a maritime Antarctic lake undergoing eutrophication. *Journal of Plankton Research*, **21**, 2393-2419.
- Chevrier, M., Vernon, P. and Frenot, Y. (1997) Potential effects of two alien insects on a subantarctic wingless fly in the Kerguelen islands, in B. Battaglia, J. Valencia and D.W.H. Walton (eds.), *Antarctic Communities: Species, Structure and Survival*. Cambridge University Press, Cambridge, UK, pp. 424-431.
- Chown, S.L. and Convey, P. (2006) Biogeography, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes, (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*. Springer, Dordrecht (this volume)
- Chown, S.L., Gremmen, N.J.M. and Gaston, K.J. (1998) Ecological biogeography of Southern Ocean islands: Species-area relationships, human impacts, and conservation, *American Naturalist* **152**, 562-575.
- Clapperton, C.M. and Sugden, D.E. (1982) Late quaternary glacial history of George VI Sound area, West Antarctica, *Quaternary Research* **18**, 243-267.
- Clapperton, C.M. and Sugden, D.E. (1988) Holocene glacier fluctuations in South America and Antarctica, *Quaternary Science Reviews* **7**, 185-198.
- Clarke, A. and Crame, A. (1989) The Origins of the Southern Ocean Marine fauna, in J.A. Crame (ed), *Origins and Evolution of the Antarctic Biota*, Geological Society Special Publication No 47, pp 253-268.
- DeConto, R. M. and Pollard, D., (2003) Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO₂, *Nature* **421**, 245-249.
- Convey, P. (1996) The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota, *Biological Reviews* **71**, 191-225.
- Convey, P. (2003) Maritime Antarctic climate change: signals from terrestrial biology. In E. Domack, A. Burnett, A. Leventer, P. Convey, M. Kirby and R. Bindshadler (eds.), *Antarctic Peninsula Climate Variability: Historical and Palaeoenvironmental Perspectives*, Antarctic Research Series, Vol. 79, American Geophysical Union, Washington, D.C., pp. 145-158.

- Convey, P. (2006) Antarctic climate change and its influences on terrestrial ecosystems, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds), *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume)
- Convey, P. and McInnes, S.J. (2005) Exceptional tardigrade-dominated ecosystems in Ellsworth Land, Antarctica. *Ecology* **86**, 519-527.
- Convey, P., Greenslade, P. and Pugh, P.J.A. (2000b) Terrestrial fauna of the South Sandwich Islands, *Journal of Natural History* **34**, 597-609.
- Convey, P., Chown, S.L., Wasley, J. and Bergstrom, D.M. (2006b) Life history traits, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Convey, P., Frenot, Y., Gremmen, N. and Bergstrom, D.M. (2006a) Biological invasions, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Convey, P., Smith, R.I.L., Hodgson, D.A and Peat, H.J. (2000a) The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating, *Journal of Biogeography* **27**, 1279-1295.
- Cromer, L., Gibson, J.A.E., Swadling, K.M. and Hodgson, D.A. (2006) Evidence for a lacustrine faunal refuge in the Larsemann Hills, East Antarctica, during the Last Glacial Maximum, *Journal of Biogeography* (in press).
- Doran P.T., Priscu J.C., Berry Lyons W., Powell R.D., Andersen D.T., Poreda R.J. (2004) Paleolimnology of extreme cold terrestrial and extraterrestrial environments, in R. Pienitz, M.S.V. Douglas, J.P. Smol (eds.), *Developments in Palaeoenvironmental Research. Volume 8. Long-term Environmental Change in Arctic and Antarctic Lakes*, Springer, Dordrecht, p 475-507
- Doran, P.T., Priscu J.C., Lyons, W.B., Walsh, J.E., Fountain, A.G., McKnight, D.M., Moorhead, D.L., Virginia, R.A., Wall, D.H., Clow, G.D., Fritsen, C. H., McKay, C. P., Parsons, A.N. (2002) Antarctic climate cooling and terrestrial ecosystem response. *Nature* **415**, 517-520.
- EPICA, (2004) Eight glacial cycles from an Antarctic ice core, *Nature*, **429**, 623-628.
- Ernsting, G., Block, W., MacAlister, H., and Todd, C. (1995) The invasion of the carnivorous carabid beetle *Trechisibus antarcticus* on South Georgia (sub-Antarctic) and its effect on the endemic herbivorous beetle *Hydromedion sparsutum*. *Oecologia* **103** 34-42.
- Feldmann, R.M. and Woodburne, M.O. (eds.) (1988) Geology and paleontology of Seymour Island, Antarctic Peninsula, *Geological Society of America Memoir* **169**, 566pp.
- Fink, D., McKelvey, B., Hannan, D., and Newsone, D. (2000) Cold rock, hot sands: In-situ cosmogenic applications in Australia at ANTARES, *Nuclear Instruments and Methods in Physics Research*, **B**, **172**, 838-846.
- Fitch, S., Lock, A., Klok, C.J., Kiernan, K. and McConnell, A. (2001) Heard Island (Indian Ocean) Photographs of upper slopes substantiate reports of activity from two distinct vents, *Bulletin of the Global Volcanism Network*, **26**, 10-11.
- Fowbert, J.A. and Smith, R.I.L. (1994) Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula, *Arctic and Alpine Research*, **26**, 290-296.
- Fox, A.J. and Cooper A.P.R. (1994) Measured properties of the Antarctic ice sheet derived from the SCAR Antarctic digital database, *Polar Record*, **30**, 201-206.
- Francis, J.E. and Poole, I. (2002) Cretaceous and early Tertiary climates of Antarctica: evidence from fossil wood. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **182**, 47-64.
- Freckman, D.W and Virginia, R.A. (1996) Low-diversity antarctic soil nematode communities: distribution and response to disturbance, *Ecology* **78**, 363-369.
- Frenot, Y., Bergstrom, D.M., Gloaguen, J.C., Tavenard, R. and Strullu D.G. (2005b) The first record of mycorrhizae on subantarctic Heard Island: a preliminary examination, *Antarctic Science*, **17**, 205-217.
- Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P., Convey, P., Skotnicki, M. and Bergstrom, D. (2005a) Biological invasions in the Antarctic: extent, impacts and implications, *Biological Reviews*, **80**, 45-72.

- Gibson, J.A.E., Wilmotte, A., Taton, A., Van De Vijver, B., Beyens, L. and Dartnall, H.J.G. (2006) Biogeographic trends in Antarctic lake communities, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.), *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Gladchenko, T.P. and Coffin, M.F. (2001) Kerguelen Plateau crustal structure and basin formation from seismic and gravity data, *Journal of Geophysical Research*, **18**, 16583-16601.
- Gore D.B., Rhodes E.J., Augustinus P.C., Leishman M.R., Colhoun E.A. and Rees-Jones J. (2001) Bunger Hills, East Antarctica: Ice free at the Last Glacial Maximum, *Geology*, **29**:1103-1106.
- Greve, M., Gremmen, N.J.M., Gaston, K.J. and Chown, S.L. (2005) Nestedness of South Ocean island biotas: ecological perspectives on a biogeographical conundrum. *Journal of Biogeography* **32**, 155-168.
- Grobe, C.W., Ruhland C.T. and Day T.A. (1997) A new population of *Colobanthus quitensis* near Arthur Harbor, Antarctica: correlating recruitment with warmer summer temperatures. *Arctic and Alpine Research* **29**, 217-221.
- Hennion, F., Huiskes, A.H.L., Robinson, S. and Convey, P. (2006) Physiological traits of organisms in a changing environment, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Hodgson, D.A. and Johnston, N.M. (1997) Inferring seal populations from lake sediments, *Nature*, **387**, 30-31.
- Hodgson D.A., Doran P.T., Roberts D. and McMinn A. (2004) Paleolimnological studies from the Antarctic and subantarctic islands, in R. Pienitz, M.S.V. Douglas, J.P. Smol (eds.), *Developments in Palaeoenvironmental Research. Volume 8. Long-term Environmental Change in Arctic and Antarctic Lakes*, Springer, Dordrecht, pp 419-474
- Hodgson D.A., Verleyen E., Squier A.H., Sabbe K., Keely B.J., Saunders K.M. and Vyverman W. (2006) Interglacial environments of coastal east Antarctica: comparison of MIS 1 (Holocene) and MIS 5e (Last Interglacial) lake-sediment records. *Quaternary Science Reviews*, **25**, 179-197.
- Hodgson D.A., Verleyen E., Sabbe K., Squier A.H., Keely B.J., Leng M.J., Saunders K.M. and Vyverman W. (2005) Late Quaternary climate-driven environmental change in the Larsemann Hills, east Antarctica, multi-proxy evidence from a lake sediment core, *Quaternary Research* **64**, 83-99
- Hodgson D.A., Noon P.E., Vyverman W., Bryant C.L., Gore D.B., Appleby P., Gilmour M., Verleyen E., Sabbe K., Jones V.J., Ellis-Evans J.C. and Wood P.B. (2001) Were the Larsemann Hills ice-free through the Last Glacial Maximum? *Antarctic Science* **13**, 440-454.
- Hughes, K.A., Ott, S., Bölter, M. and Convey, P. (2006) Colonisation processes, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Huiskes, A.H.L., Convey, P. and Bergstrom, D.M. (2006) Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Jouzel J., Barkov N.I., Barnola J.M., Bender M., Chapellaz J., Genthon C., Kotlyakov V.M., Lipenkov V., Lorius C., Petit J.R., Raynaud D., Raisbeck G., Ritz T., Sowers C., Stievenard M., Yiou F. and Yiou P. (1993) Extending the Vostock ice-core record of palaeoclimate to the penultimate glacial period, *Nature* **364**, 407-412
- Kennedy, A.D. (1993) Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis, *Arctic and Alpine Research* **25**, 308-315.
- Kennett, J.P. (1977) Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography, *Journal of Geophysical Research* **82**, 3843-3860.
- Larter, R.D. and Vanneste, L.E. (1995) Relict subglacial deltas on the Antarctic Peninsula outer shelf, *Geology* **23**, 33-36.
- Laursen, G.A., Treu, R., Seppelt, R.D. and Stephenson, S.L. (1997) Mycorrhizal assessment of vascular plants from subantarctic Macquarie Island, *Arctic and Alpine Research* **29**, 483-491.

- LeMasurier, W.E. and Thomson, J.W. (1990) Volcanoes of the Antarctic Plate and Southern Oceans. *American Geophysical Union, Antarctic Research Series* **48**, 487 pp.
- Livermore, R.A., Nankivell, A.P., Eagles, G. and Morris, P. (2005) Paleogene opening of Drake Passage. *Earth and Planetary Science Letters* **236**, 459-470.
- Longton, R.E. (1988) *The biology of polar bryophytes and lichens*, Cambridge University Press, Cambridge, 391 pp.
- Lyons, W.B., Laybourn-Parry, J., Welch, K.A. and Priscu, J.C. (2006) Antarctic lake systems and climate change, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Marshall, D.J. and Coetzee, L. (2000) Historical biogeography and ecology of a Continental Antarctic mite genus, *Maudheimia* (Acari, Oribatida): evidence for a Gondwanan origin and Pliocene-Pleistocene speciation, *Zoological Journal of the Linnean Society* **129**, 111-128.
- Marshall, D.J. and Convey, P. (2004) Latitudinal variation in habitat specificity of ameronothroid mites. *Experimental and Applied Acarology* **34**, 21-35.
- Marshall, D.J. and Pugh, P.J.A. (1996) Origin of the inland Acari of Continental Antarctica, with particular reference to Dronning Maud Land, *Zoological Journal of the Linnean Society* **118**, 101-118.
- McLoughlin, S. (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism, *Australian Journal of Botany* **49**, 271-300.
- Muñoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. and Martínez, I. (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* **304**, 1144-1147.
- Nolan, L., Hogg, I.D., Stevens, M.I. and Haase, M. (In press) Molecular support for a secondary contact zone among glacial refugia for the springtail *Gomphiocephalus hodgsoni* (Collembola) in Taylor Valley, continental Antarctica, *Polar Biology*.
- Ó Cofaigh, C., Pudsey, C.J., Dowdeswell, J.A. and Morris, P. (2002) Evolution of subglacial bedforms along a paleo-ice stream, Antarctic Peninsula continental shelf, *Geophysical Research Letters* **29**, 1199, doi: 10.1029/2001GLO14488.
- Peat, H.J., Clarke, A. and Convey, P. (in press) Diversity and biogeography of the Antarctic flora. *Journal of Biogeography*.
- Peck, L.S., Clark, M.S., Clarke, A., Cockell, C.S., Convey, P., Detrich III, H.W., Fraser, K.P.P., Johnston, I.A., Methé, B.A., Murray, A.E., Römisch, K. and Rogers, A.D. (2005) Genomics: applications to Antarctic Ecosystems, *Polar Biology* **28**, 351-365.
- Pickard, J. and Seppelt, R.D. (1984) Phytogeography of Antarctica. *Journal of Biogeography* **11**, 83-102.
- Poole, I. and Cantrill D.J. (2001) Fossil wood from Williams Point beds, Livingston Island, Antarctica: a late Cretaceous southern high latitude flora, *Palaeontology* **44**, 1081-1112.
- Pugh, P.J.A., Dartnall, H.J.G. and McInnes, S.J. (2002) The non-marine Crustacea of Antarctica and the Islands of the Southern Ocean: biodiversity and biogeography, *Journal of Natural History*. **36**, 1047-1103
- Quesada, A., Vincent, W.F. Kaup, E., Hobbie, J.E., Laurion, I., Pienitz, R., López-Martínez, J. and Durán, J.-J. (2006) Landscape control of high-latitude lakes in a changing climate, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Scher, H.D. and Martin, E.E. (2006) Timing and climatic consequences of the opening of Drake Passage. *Science*, **312**, 428-430.
- Schwab, M.J. (1998) Rekonstruktion der spätquartären Klima- und Umweltgeschichte der Schirmacher Oase und des Wohlthat Massivs (Ostantarktika), *Berichte zur Polarforschung* **293**, 1-128.
- Selkirk, P.M., Seppelt, R.D. and Selkirk, D.R. (1990) *Subantarctic Macquarie Island. Environment and Biology*. Studies in Polar Research Cambridge University Press, Cambridge, 285 pp.
- Skotnicki, M.L. and Selkirk, P.M. (2006) Plant biodiversity in an extreme environment: genetic studies of origins, diversity and evolution in the Antarctic, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).

- Skottsberg, C. (1904) On the zonal distribution of South Atlantic and Antarctic Vegetation, *Geography Journal* **24**, 655-663.
- Smith, R.I.L. (1984) Terrestrial Plant Biology of the Subantarctic and the Antarctic, in R.M. Laws (ed.), *Antarctic Ecology* Volume 1, Academic Press, London, pp. 61-162.
- Smith, R.I.L. (1988) Destruction of Antarctic terrestrial ecosystems by a rapidly increasing fur seal population, *Biological Conservation* **45**, 55-72.
- Smith, R.I.L. (2005) The bryophyte flora of geothermal habitats on Deception Island, Antarctica, *Journal of the Hattori Botanical Laboratory* **97**, 233-248.
- Smith, R.I.L. and Convey, P. (2002) Enhanced sexual reproduction in bryophytes at high latitudes in the maritime Antarctic, *Journal of Bryology* **24**, 107-117.
- Stevens, M.I. and Hogg, I.D. (2003) Long-term isolation and recent range expansion from glacial refugia revealed for the endemic springtail *Gomphiocephalus hodgsoni* from Victoria Land, Antarctica. *Molecular Ecology* **12**, 2357-2369.
- Stevens, M.I. and Hogg, I.D. (2006) The molecular ecology of Antarctic terrestrial and limnetic invertebrates and microbes, in D.M. Bergstrom, P. Convey, and A.H.L. Huiskes (eds.) *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, Springer, Dordrecht (this volume).
- Tripati, A., Backman, J., Elderfield, H. and Ferretti, P. (2005) Eocene bipolar glaciation associated with global carbon cycle changes, *Nature* **436**, 3410346.
- Truswell, E.M., Quilty P.G., McMinn A., Macphail M.K., Wheller G.E. (2005) Late Miocene vegetation and palaeoenvironments of the Drygalski Formation, Heard Island, Indian Ocean: evidence from palynology, *Antarctic Science* **17**, 427-422 doi: 10.1017/S0954102005002865.
- Turner P.A.M., Scott J.J. and Rozefelds A. (2006) Probable long distance dispersal of *Leptinella plumosa* Hook. f. to Heard Island: habitat, status and discussion of its arrival, *Polar Biology*, **29**, 160-168.
- Wall, D.H. (In press) Above-Belowground Interactions in a Low Diversity Ecosystem: The McMurdo Dry Valleys, *Philosophical Transactions of the Royal Society*.
- Walton, D.W.H. (1984) The terrestrial environment, in R.M. Laws (ed), *Antarctic Ecology* Volume 1. Academic Press, London, pp 1-60.
- Whinam, J., Chilcott, N. and Bergstrom, D.M. (2004) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms, *Biological Conservation* **121**, 207-219.
- Williams, P.G., Roser, D.J. and Seppelt, R.D. (1994) Mycorrhizae of hepatics in continental Antarctica, *Mycological Research* **98**, 34-36.
- Williams, M., Dunkerley, D., DeDeckker, P., Kershaw, P. and Chappell, J. (1998) *Quaternary Environments*, Arnold, London, 352 pp.