

Antarctic Terrestrial Ecosystems: Responses to Environmental Change

by Peter Convey¹

Abstract: The consequences of climate change are exciting considerable concern worldwide. Parts of Antarctica are facing the most rapid rates of anthropogenic climate change currently seen on the planet. This paper sets out to introduce contemporary ecosystems of the Antarctic, and the factors that have influenced them and their biodiversity over evolutionary timescales. Contemporary climate change processes significant to terrestrial biota, and the biological consequences of these changes seen to date, are described. In general, many Antarctic terrestrial biota, when considered in isolation, possess biological features that will permit them to take advantage of the levels of change currently being experienced. However, many organisms and communities are extremely vulnerable to the colonisation of new taxa with greater competitive abilities or representing higher trophic levels than are currently present amongst the indigenous biota. In this context, direct human impact in the form of accidental transfer of non-indigenous species is probably the greatest threat currently facing Antarctic terrestrial ecosystems and their biota, while climate change will also act synergistically to reduce the colonisation and establishment hurdles faced by incoming organisms.

Zusammenfassung: Die Konsequenzen des Klimawandels erregen weltweit beträchtliche Bedenken. Teile der Antarktis stehen dem schnellsten, vom Menschen verursachten, Klimawandel gegenüber, der bisher auf der Erde beobachtet wurde. Dieser Artikel will eine Einleitung geben in das derzeitige Ökosystem der Antarktis, in die Faktoren, die dieses beeinflusst haben, und in die Biodiversität im Wandel der Zeit. Derzeitige Prozesse des Klimawandels, bedeutend für terrestrische Lebewesen, und die bisher sichtbaren biologischen Konsequenzen dieses Wandels werden beschrieben. Im allgemeinen besitzen antarktische Lebewesen biologische Merkmale, die es ihnen erlauben, Vorteile aus dem derzeitigen Stand des Wandels zu ziehen. Viele Organismen und Gemeinschaften sind jedoch extrem verwundbar in Hinblick auf die Besiedlung durch neue Arten, die entweder größere Durchsetzungsmöglichkeiten haben oder einen höheren Platz in der Nahrungskette einnehmen als die derzeit vorkommenden einheimischen Arten. In diesem Zusammenhang ist der direkte menschliche Einfluss durch die ungewollte Einschleppung fremder Arten die größte Bedrohung des antarktischen terrestrischen Ökosystems und dessen Lebewesen, während der Klimawandel zusätzlich die Hürden reduziert, die eine erfolgreiche Besiedlung und Etablierung eindringender Organismen behindern.

INTRODUCTION TO ANTARCTIC TERRESTRIAL ECOSYSTEMS

In the context of terrestrial biology, Antarctic terrestrial environments, here taken to include the major sub-Antarctic islands, are characterised as including all exposed ground south of approximately 50 °S latitude (Fig. 1). In a region of this size, many different terrestrial ecosystems are present. Various biogeographical schemes have been suggested as a means of classifying these, but there is currently a general recognition of three biogeographical zones within the Antarctic as a whole, the sub-, maritime and continental (or frigid) Antarctic (SMITH 1984, LONGTON 1988, CHOWN & CONVEY in press). While the biological and climatic characteristics of these three zones are distinct (Tab. 1) and they provide a useful background to the region for the unfamiliar, it is also the case

that recent research indicates that a significant refining of our understanding of Antarctic biogeography is now underway, a subject discussed in more detail below (see also CHOWN & CONVEY 2006, in press, PEAT et al. 2007, CONVEY in press).

The sub-Antarctic zone includes isolated islands and archipelagos at high latitudes in the Southern Ocean. Most, with the exception of South Georgia, Heard and McDonald Islands, are close to or north of the oceanic Polar Frontal Zone. These islands are under strong maritime influence, which limits and buffers temperature variation year round, as they are not normally impacted by pack or fast ice. The maritime Antarctic is also a region under strong maritime influence from the Southern Ocean, in this case with the influence being more seasonal in nature and limited to the short Antarctic summer period. It includes the western coast of the Antarctic Peninsula to c. 72 °S, the South Shetland, South Orkney and South Sandwich Islands, and the isolated Bouvetøya and Peter I Øya. The central mountain spine, eastern coast and the more southern elements of the Antarctic Peninsula are not included, and therefore the term “maritime Antarctic” does not include all, or even a majority of, the geological region of West Antarctica. The continental Antarctic is the largest biogeographical zone in terms of area, including all of East Antarctica, the Balleny Islands, and those parts of the Antarctic Peninsula not included in the maritime Antarctic. By contrast with the other two zones, terrestrial habitats of the continental Antarctic are very limited in extent and more isolated, although they include coastal rocky regions superficially similar to those of the maritime Antarctic. One exception here is formed by the extensive ice-free cold deserts of Victoria Land (LYONS et al. 1997). Air temperatures in the continental Antarctic are more extreme than those of the maritime and sub-Antarctic although, as in all zones, microhabitat temperatures may be more variable, in particular with snow cover giving protection from winter thermal minima. During the brief summer, absorption of energy by rocks and soil can lead to melting and free water being available even at the most southern ice-free locations.

The Antarctic terrestrial biota is generally described as being depauperate in terms of species numbers in comparison with virtually all other environments worldwide, with many familiar groups missing completely or very poorly represented (BLOCK 1984, SMITH 1984, CONVEY 2001, in press). Thus terrestrial vertebrates are hardly present, and then limited to the sub-Antarctic (all birds: one passerine, two ducks, two scavenging sheathbills). The abundance of marine mammals, particularly in the sub-Antarctic but also in parts of the maritime and continental Antarctic coastline, can generate considerable impacts locally on terrestrial ecosystems (manuring, aerosol nutrient dispersal, trampling). Similarly, with a single

¹ British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK; <p.convey@bas.ac.uk>

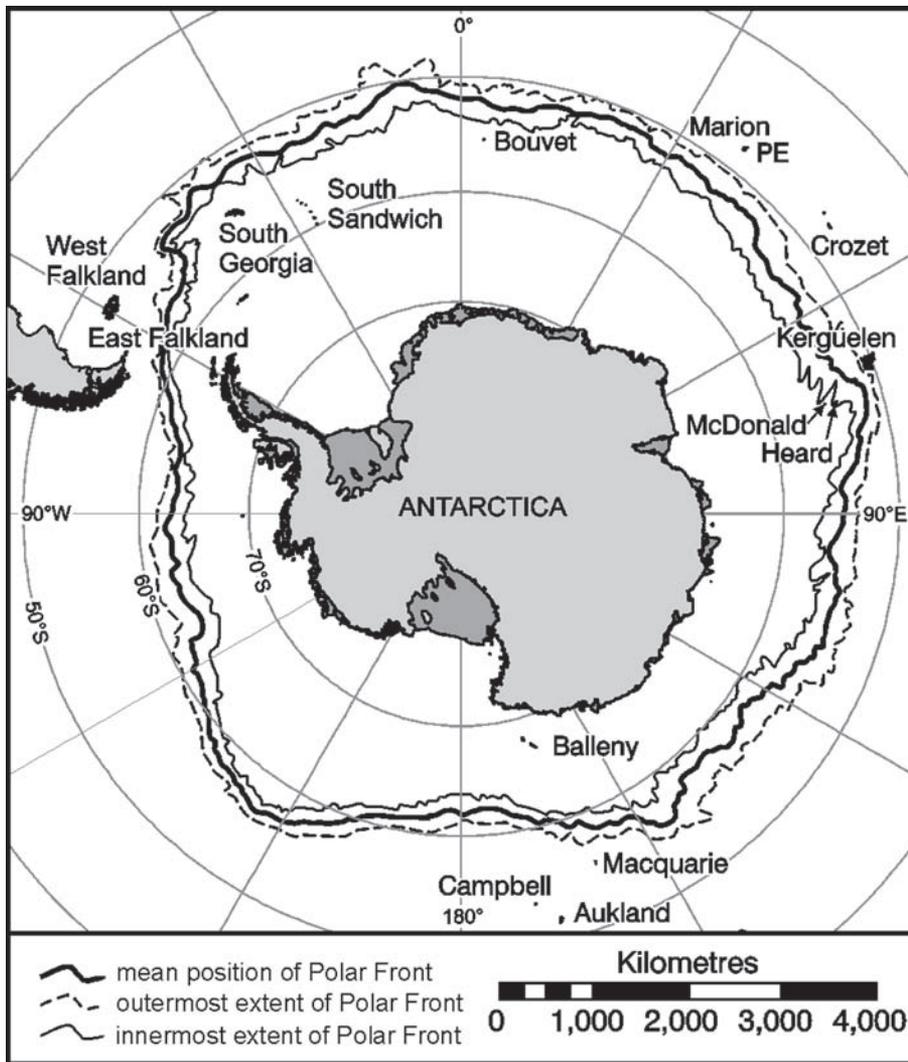


Fig. 1: General map of the Antarctic region, including the major sub-Antarctic islands and the typical position of the oceanic polar frontal zone (from BARNES et al. 2006).

Abb. 1: Die Antarktis und die größeren subantarktischen Inseln, sowie die typische Lage der ozeanischen Polarfrontzone (nach BARNES et al. 2006).

	Months with positive mean air temperature	Typical air temperature ranges (°C)		Day degrees above zero
		Mean winter to summer	Extreme range	
High Arctic	2 to 4	-34 to +5	-60 to +20	50-350
Sub-Antarctic	6 to 4	-2 to +8	-10 to +25	700-1700
Maritime Antarctic	1 to 4	-12 to +2	-45 to +15	6-100
Continental Antarctic coast	0 to 1	-30 to -3	-40 to +10	0
Continental Antarctic inland	0	<-50 to -10	<-80 to -10	0

Tab. 1: Typical ranges in thermal characteristics of major regions of Antarctica, with comparative data included for the High Arctic. To provide greater information, the continental Antarctic biogeographical zone has been split to give separate data on its coastal and inland regions. The measure of physiological time is based on air temperature data, and will underestimate thermal energy available at microhabitat scale, at least during the summer months and periods of direct insolation. (Table modified from CONVEY 2006).

Tab. 1: Typische Temperaturbereiche der antarktischen Regionen im Vergleich mit der Arktis. Die biogeographische Region "kontinentale Antarktis" wurde in zwei Regionen unterteilt, um separate Daten für die Küsten und das Binnenland anzugeben. Die Messung der physiologisch aktiven Zeit basiert auf Lufttemperaturdaten und unterschätzt die den Mikrohabitaten bereitstehende Wärmeenergie, insbesondere in den Sommermonaten und den Zeiten der direkten Isolation. (Tabelle modifiziert nach CONVEY 2006).

exception (the diminutive dwarf shrub *Coprosina* on Macquarie Island), woody trees and shrubs are absent. Animal communities are dominated by invertebrates, and plants by cryptogamic groups. Many authors have recognised that biodiversity and community complexity decrease with progression towards more extreme environmental conditions through the three zones, although this large scale pattern is not always mirrored in detail by within-zone patterns (CHOWN & CONVEY 2006, in press, CONVEY 2001, in press, CLARKE 2003) (Tab. 2). Even in the sub-Antarctic, higher taxonomic level invertebrate

diversity is very limited, with insect orders other than Diptera (flies) and Coleoptera (beetles) rarely encountered even where indigenous representatives are known (GRESSITT 1970, GREENSLADE 2006). At regional scale, even though it is known that diverse micro-arthropod (Acari, Collembola) and micro-invertebrate (Nematoda, Tardigrada, Rotifera) communities exist (BLOCK 1984), finer scale data are generally not available and much remains to be learnt of the biology and distribution of these groups. Some Antarctic faunal communities are recognised as amongst the simplest on the planet (FRECKMAN &

Group	Sub	Maritime	Continental
Protozoa	83		33
Rotifera	> 59	> 50	13
Tardigrada	> 34	26	19
Nematoda	> 22	28	14
Platyhelminthes	4	2	0
Gastrotricha	5	2	0
Annelida (Oligochaeta)	23	3	0
Mollusca	3/4	0	0
Crustacea (terrestrial)	4	0	0
Crustacea (non-marine)	44	10	14
Insecta (total)	210	35	49
(Mallophaga)	61	25	34
(Diptera)	44	2	0
(Coleoptera)	40	0	0
Collembola	> 30	10	10
Arachnida (total)	167	36	29
(Araneida)	20	0	0
(Acarina)	140	36	29
Myriapoda	3	0	0
Flowering plants	60	2	0
Ferns, clubmosses	16	0	0
Mosses	250	100	25
Liverworts	85	25	1
Lichens	250	250	150
Macro-fungi	70	30	0

Tab. 2: Current knowledge of levels of biodiversity within the three Ant-arctic biogeographical zones (collated from CONVEY in press).

Tab. 2: Derzeitiger Wissensstand zur Biodiversität in den drei antarktischen biogeographischen Zonen. (Vergleichbare Daten siehe CONVEY im Druck).

VIRGINIA 1997), in some large geographical areas lacking even the nematode worms, a group previously thought to be ubiquitous in faunal communities worldwide (CONVEY & MCINNES 2005). However, even the simplest faunal communities yet described from the Antarctic include representatives of both primary consumer and predatory trophic levels. Both vascular plants and ferns are relatively well represented in the sub-Antarctic, the former including representatives of the “mega-herb” growth form whose evolution appears to have been encouraged by the lack of native vertebrate herbivores (MITCHELL et al. 1999, CONVEY et al. 2006a). Their regional diversity is much lower than is present at northern hemisphere (including Arctic) sites at comparable latitudes, or that face similar or much more extreme environmental conditions. Thus, native vascular plants diversity on the Svalbard archipelago alone (c. 76-80 °N, isolated by >1000 km from Scandinavia – RØNNING 1996) is greater than recorded across the entire sub-Antarctic region (at less than 55 °S). Only two vascular plants are known from the entire Antarctic continent, both restricted to coastal regions of the Antarctic Peninsula. These two plants, along with many of the bryophytes present in the Antarctic, have South American (Andean) distributions extending well beyond Antarctica.

Trophic structure of Antarctic terrestrial ecosystems is very simple. Even in the sub-Antarctic, the majority of invertebrates are thought to be microbivores or detritivores, and predation pressure is minimal (although these generalisations suffer from an important caveat in the lack of specific and rigorous autecological study of most members of most communities at any location across the Antarctic – HOGG et al. 2006). As an example, terrestrial arthropod predators in the

maritime Antarctic are represented by at most two species of prostigmatid and mesostigmatid mite at any location, which are often not encountered using standard field collection techniques. Detailed studies of one of these species failed to demonstrate a functional response when presented with even the minimum natural density of the primary prey (a species of springtail), suggesting that their ecological role is currently insignificant (LISTER et al. 1988, USHER et al. 1989). The lack of true herbivores is also unusual on a global scale – although the underlying reasons have not been probed in detail, it is possibly as a result of energetic constraints (LEATHER et al. 1993).

Vegetation over much of the Antarctic is very sparse. Scree, boulder fields and simple soils are colonised by cryptogamic “fellfield” vegetation (mosses, liverworts, lichens) (SMITH 1984). These may develop, in favourable locations, into closed plant communities, and occasionally moss peat deposits may develop. These are known from a very small number of locations in the maritime Antarctic, with maximum radiocarbon ages of c. 5-6000 years (FENTON & SMITH 1982, BJÖRK et al. 1991). On sub-Antarctic South Georgia, which was very extensively glaciated as the Last Glacial Maximum, maximum deposit ages of c. 14000 years have been reported recently (VAN DER PUTTEN & VERBRUGGEN 2005), although older ages must be expected from other sub-Antarctic islands, some of which have not undergone complete glaciation.

While biogeographical data available for macrofauna and flora are far from complete, they compare well with the minimal information available for most microbial groups. Despite the recognition that microbial autotrophs are fundamental to polar terrestrial ecosystem processes (VINCENT 1988, WYNN-WILLIAMS 1993, 1996a), as they are worldwide, the geographical coverage of microbial studies in the Antarctic as a whole is very sparse. As well as being primary colonists and sometimes the only primary producers or biota present, fungi, algae and cyanobacteria are also important in stabilizing mineral soils, and in the development of suitable substrata for secondary colonists. In recent years, the application of techniques for measuring molecular diversity and investigating the molecular phylogeny of microbial groups has started to lead to a rapid expansion in diversity data available (LAWLEY et al. 2004, ADAMS et al. 2006, YERGEAU et al. 2006). These studies are already challenging conventional understanding of patterns of Antarctic diversity and, particularly in the context of microbiology, challenging the predictions of the “global ubiquity hypothesis” (FINLAY 2002, BOENIGK et al. 2006).

Microbial communities are present across the Antarctic (VINCENT 1988). As well as terrestrial habitats, they are also found in cryophilic habitats such as in snow. Along with a few metazoans – tardigrades and protozoans – microbes also occupy cryoconite holes that develop in glacier surfaces (CHRISTNER et al. 2003, MUELLER & POLLARD 2004). Chasmo-lithic and endolithic microbial communities are found within the surface layers of some sandstones and other light transmitting minerals such as gypsum (FRIEDMANN 1982, HUGHES & LAWLEY 2003). These may represent one limit to biological existence on Earth, and have been a focus of attention in the field of exobiology, as models for the possible continuing existence of life on other planetary systems.

SPATIAL AND TEMPORAL INFLUENCES ON ANTARCTIC TERRESTRIAL BIODIVERSITY

Antarctica formed a central element of the Gondwanan supercontinent. As the different elements separated to give the continents with which we are familiar today, the final links to break were with Australia and South America, separating 30-35 million years ago (LIVERMORE et al. 2005, BERGSTROM et al. 2006). The physical isolation of Antarctica allowed circum-Antarctic oceanic and atmospheric circulation patterns to develop, further isolating the continent from heat transfer from lower latitudes and accelerating the processes of continental cooling. However, while these oceanic and atmospheric circulation patterns certainly restrict the transfer of biota into and out of Antarctica, it is clear that low levels of transfer have continued since their establishment (CLARKE et al. 2005, BARNES et al. 2006). Fossil evidence also indicates that a cool temperate fauna and flora comparable to those of southern South America and Australia/New Zealand survived in Antarctica for many millions of years after continental isolation, well after the commencement of glaciation (CLARKE & CRAME 1989, POOLE & CANTRILL 2001). Contemporary ice extent means that, inevitably, the fossil record available from Antarctica is very incomplete, but there is clear evidence that, as recently as 8-10 million years ago and possibly more recently, areas of *Nothofagus* dwarf scrub were present on the continent. It is also becoming clear that, while the extent of glaciation and ice sheet formation has varied widely over time, current models do not give sufficient accuracy or precision in determining their boundaries to allow integration of biological and glaciological fields of research.

The contemporary ice-free ecosystems of the 0.34 % of the Antarctic continent that does not experience continuous ice or snow cover (BAS 2004) include nunataks, cliffs and areas exposed seasonally through snow melt or ablation (scree and rubble slopes, valley bottoms, coastal plains). Habitat extent is greater, and duration of exposure longer, on the sub-Antarctic islands, some of which rarely experience extended periods of snow cover, especially at low altitudes. The typical pattern seen across the maritime and continental Antarctic zones is of ice-free areas that are small in area and isolated from other such habitat islands on a range of scales from metres to tens or hundreds of km. At the largest scale, the continent of Antarctica is isolated from South America by approaching 1000 km, and by 4-5000 km from Australia and South Africa.

In these isolated habitats, seasonal snow and ice cover can be an important influence on the level of biodiversity that is sustainable – where this cover exists habitats are buffered from extreme low temperatures and rapid fluctuations and from abrasion by wind-blown ice. In the maritime and continental Antarctic, sub-nivean temperatures are generally sufficiently low to cause biological activity to cease over winter and, indeed, at more southern locations habitats may only become snow free and biological activity be possible for days to weeks. Most sub-Antarctic islands provide a striking contrast to this pattern, as they experience only intermittent snow cover, and microhabitat temperatures can remain positive or near to freezing point year-round, allowing continuous biological activity (CONVEY 1996a).

A final important influence on levels of biodiversity relates to

soil properties, particularly in areas such as the many Antarctic locations where the development of habitats structured by macroscopic vegetation is limited or non-existent. Most Antarctic soils are poorly developed, with low organic and nutrient content (BEYER & BÖLTER 2002, LAWLEY et al. 2004, BRINKMANN et al. in press). Brown soils, familiar from lower latitudes, are only found in association with communities of vascular plants, so are of very limited representation in the maritime Antarctic, but more widespread in the sub-Antarctic (SMITH 1984). A feature of the sub-Antarctic is the presence of extensive moss peat deposits, which again are of much more restricted distribution in the maritime Antarctic, and are not present in the continental zone. Radiocarbon dating evidence points to peat deposition commencing soon after the end of Pleistocene glaciation (FENTON & SMITH 1982, BJÖRK et al. 1991, VAN DER PUTTEN & VERBRUGGEN 2005). Permafrost is widespread in the maritime and continental Antarctic, but is generally absent from most sub-Antarctic islands, except at higher altitudes on the heavily glaciated South Georgia and Heard Island. In combination with frequent freeze-thaw disturbance (cryoturbation), the result is that Antarctic soils are particularly unstable and mobile, factors affecting the ability of biological propagules to establish.

CONTEMPORARY CLIMATE AND CLIMATE CHANGE

Across the wide range of terrestrial and freshwater habitats present in the Antarctic, one common factor is generally shared – that of lying in some respect towards the extreme limits of one or more of the environmental gradients available on Earth (PECK et al. 2006). In particular, this feature is encountered in the context of many seasonally related environmental stresses – low temperature, (liquid) water availability, ice cover and light. In terms of the thermal environment, the energy available to terrestrial habitats in Antarctica is considerably less than in the Arctic, with temperatures at comparable latitudes being several degrees (at least 5-10 °C) higher in the latter, and there being no northern comparison for the conditions experienced across the vast majority of the continental Antarctic. However, towards both poles, the tight linkage between light, temperature and water at latitudes beyond the polar circles imposes comparable seasonal constraints on terrestrial biological activity.

The influence of seasonality on Antarctic terrestrial biology is complex, even though many of the features or adaptations reported are interpreted in the context of seasonal features. The extreme thermal seasonality experienced across much of the Antarctic, which increases both with latitude and with distance from the coast and the moderating influence of the surrounding ocean, restricts biological activity. Even where the thermal environment is suitable for biological activity, further limits are imposed by desiccation (governed by interactions between precipitation, snow, ice or permafrost melt, ablation), to the extent that activity may only be possible in some habitats for as little as days to weeks in a year (e.g. SØMME 1986, SCHLENSOG et al. 2004), or even not at all in some summers.

Antarctic terrestrial ecosystems experience low thermal energy input even relative to those of high northern latitudes (Tab. 1) (CONVEY 1996A, 2006, DANKS 1999). The measure of physiological time (day degrees above 0 °C) provides a basic

quantification of this difference. Such low summer temperatures are linked with low microhabitat temperatures, which can often be near to minimum threshold temperatures for specific physiological or behavioural activities. Therefore, even a small temperature increase may have an important biological impact, an interpretation consistent with predictions of extreme sensitivity to climate change.

Antarctic biota have faced climate change throughout the history of the continent. Most recently, patterns of change through the Pleistocene and Holocene are well documented (e.g. HJORT et al. 2003, EPICA 2004). However, while at a large scale the associated expansions and contractions (range and depth) of glaciers and ice sheets are well described, fine scale resolution particularly of boundary areas is less understood. Even over the last few thousand years, and before the rapid changes seen during the last several decades, there have been large fluctuations in ice extent (CLAPPERTON & SUGDEN 1982, 1988, LORIUS et al. 1985, SMITH 1990, PUDSEY & EVANS 2001).

Since the 1950s, the western Antarctic Peninsula and parts of the Scotia arc have seen some of the most rapid rates of temperature increase seen worldwide (KING et al. 2003, VAUGHAN et al. 2003). In the detailed record available from Faraday/Vernadsky Station (Argentine Islands, c. 65 °S) over this period, mirrored by other records from stations in the South Shetland and South Orkney Islands, mean annual temperature has risen at a rate of 5.7 ± 2.0 degrees centigrade per century, with much stronger warming in the winter than the summer months (though the latter is still significant). VAUGHAN (2006) has also expressed this level of warming in terms of the increase in cumulative day degrees above 0 °C, recording a 74 % increase in this value over the same period. Limnological data from maritime Antarctic Signy Island (South Orkney Islands) indicates that these macroclimatic trends can be magnified by a factor of 2 to 3 in freshwater ecosystems (QUAYLE et al. 2002, 2003), associated with changes in autumn freeze and spring ice break up that have increased the open water period by up to four weeks, and altered patterns of biological productivity and nutrient flow. Warming trends are also recorded at several sub-Antarctic locations and some along the continental coastline (SMITH & STEENKAMP 1990, SMITH 2002, FRENOT et al. 1997, TWEEDIE & BERGSTROM 2000, JACKA & BUDD 1998, VAUGHAN et al. 2001). Temperature increases along the Antarctic Peninsula and Scotia arc are linked to decreasing winter sea ice extent and to El Niño Southern Oscillation (ENSO) events (CULLATHER et al. 1996, HARANGOZO 2000). However, it is still the case that the current generation of climate models do not predict accurately these patterns of warming (KING et al. 2003).

Temperature is not the only biologically important environmental variable undergoing contemporary change. It is recognised that availability of liquid water plays perhaps an even more important role as a key environmental variable influencing distributions of polar terrestrial organisms (KENNEDY 1993, SØMME 1995, BLOCK 1996). However, although climate models predict changes in precipitation patterns, it is not yet possible to apply these at the fine spatial scale required for specific terrestrial ecosystems. This is further complicated by the fact that precipitation patterns co-vary with other environmental variables such as temperature, cloud cover and wind

speed. Predictions of precipitation increase in the Antarctic coastal zone (BUDD & SIMMONDS 1991) are supported by the limited data available from the maritime Antarctic (TURNER et al. 1997). In the maritime Antarctic summer precipitation increasingly occurs as rain rather than snow (NOON et al. 2001, QUAYLE et al. 2003), thus becoming directly available to terrestrial ecosystems. Increases in precipitation are also noted from sub-Antarctic Macquarie Island (C. TWEEDIE, D. DOLEY & D. BERGSTROM unpubl. data), while decreases have been reported from other sub-Antarctic islands including Marion Island (SMITH 2002) and Iles Kerguelen (FRENOT et al. 1997, CHAPUIS et al. 2004). Other more subtle changes in patterns of interacting environmental variables have also been reported – for example, HODGSON et al. (2006) have identified rapid changes over recent time in salinity of some coastal continental Antarctic lakes, and interpreted these as indicating a change in typical wind direction leading to greater evaporation relative to precipitation.

As with precipitation, exposure to direct insolation (i.e the receipt of photosynthetically active radiation (PAR), prerequisite for the carbon fixation by primary producers that underlies virtually all ecosystem processes) co-varies strongly with other environmental variables, meaning that any changes will have implications for primary production. Separately, the possible biological impacts of the anthropogenically generated “ozone hole” (FARMAN et al. 1985) have received much attention. Formed by a separate pollution-related process to those underlying global warming, the effect of spring damage to the stratospheric ozone layer above Antarctica has been to change exposure at the Earth’s surface to shorter wavelength ultraviolet radiation (UV-B). In particular, as well as increasing the potential for direct radiation damage to vital cellular components (e.g., chloroplasts and their integral chemical photosystems, DNA) (ROZEMA 1999), the associated increase in exposure to these shorter wavelengths alters the ratio of PAR or UV-A to UV-B, which is important for intracellular repair processes (SANTAS et al. 1997). Maximum UV-B exposure levels during the ozone hole are comparable to those experienced at mid-summer, and their significance lies in their timing – when many organisms remain in their winter period of inactivity – rather than absolute magnitude (CONVEY 2006).

BIOGEOGRAPHICAL PATTERNS IN MAJOR FLORA, FAUNA AND MICROBIAL GROUPS

Any attempt to describe terrestrial biogeographical patterns within Antarctica quickly encounters two fundamental problems. First, sampling coverage is poor at best and completely inadequate at worst. Even for the better known groups (e.g. microarthropods, bryophytes, lichens), many locations remain to be visited – in a study examining patterns in probably the best-surveyed components of Antarctic terrestrial biota (bryophytes and lichens) PEAT et al. (2007) illustrate that, on as large a scale as one degree by one degree latitude-longitude “boxes”, records exist only for 50 % of the boxes known to include at least 100 m² of ice free ground (and even where such records do exist, they do not imply complete coverage within a box, or that specific locations have been surveyed or visited by a specialist). For many less known groups current knowledge relies on data from a very few or even single sites, often associated with the field activities of a specific taxono-

mist. Generally across the continent, particularly at inland locations and remote from permanent research stations, there has been virtually no targeted collecting activity or field visits by trained biological specialists. Second, taxonomic uncertainty (e.g. synonymy, undescribed and/or cryptic species) is present to some extent in all groups encountered (see MASLEN & CONVEY 2006) for a recent example pertaining to nematode worms). Resolution of this limitation requires considerably greater research effort than has been applied to date, and the application of classical and molecular phylogenetic techniques in tandem.

The availability of molecular biological approaches to studies of microbial diversity and taxonomy promise an imminent acceleration in the level of data available (LAWLEY et al. 2004, BOENIGK et al. 2006, ADAMS et al. 2006, YERGEAU et al. 2006). This will allow a meaningful test of the currently popular “global ubiquity hypothesis”, which postulates that, since many microbes are very effective dispersers (through a combination of small size leading to ease of movement into the air column, and the possession of resistance adaptations), there should be more evidence of ubiquitous microbial species distributions than is the case for larger organisms. The evidence currently available is contradictory. Classical studies of Antarctic algae and fungi indicate the presence of many cosmopolitan taxa (PEGLER et al. 1980, BROADY 1996, VISHNIAC 1996). However, molecular studies give evidence for considerable isolation and lack of exchange at intra- and inter-continental scales (FRANZMANN 1996), both within species (BOENIGK et al. 2006) and at the level of communities (LAWLEY et al. 2004).

Large-scale biogeographical patterns are clearly visible in the distributions of at least some Antarctic macrobiota. Recent analyses of patterns across the islands of the Southern Ocean surrounding Antarctica, including those of the sub- and maritime Antarctic and more northern cold temperate islands, have confirmed the importance of wind dispersal (MUÑOZ et al. 2004, CHOWN & CONVEY 2006, in press). At a local scale, a typical range of factors encountered in studies of island biogeography worldwide (e.g., climate, area, vegetation type, human occupancy) influence the richness of specific groups (CHOWN et al. 1998, SELMI & BOULINIER 2001, CHOWN & CONVEY 2006, in press). However, although the potential for aerial dispersal to Antarctica from lower southern latitudes (GRESSITT et al. 1960; MARSHALL 1996) or within Antarctica (HUGHES et al. 2004) has been demonstrated, pattern analyses of this type have yet to be extended to most of the mainland of the Antarctic Peninsula or continent.

With reference to the biogeographical history of the latter regions, contemporary views are changing rapidly. GRESSITT (1965, 1971) recognised that elements of the Antarctic terrestrial biota probably had two separate origins – an ancient component that has survived throughout the episodes of glaciation in Antarctica, and a recent component, most likely to have colonised following ice retreat at the end of the Pleistocene. This view plainly has currency in parts of the continental Antarctic known to have remained at least in part ice free since 10-12 Ma in the Miocene (parts of the southern Victoria Land Dry Valleys and the Transantarctic Mountains – BOYER 1979, PRENTICE et al. 1993), and for inland nunatak refuges (e.g. MARSHALL & PUGH 1995, MARSHALL & COETZEE

2000). However, a widely held view has developed that most other Antarctic terrestrial habitats and biota must be more recent in origin, as most terrestrial biota in all three biogeographical zones (especially the sub- and maritime Antarctic) are found only in coastal, low altitude locations. Along the continental coastline, the maritime Antarctic and those sub-Antarctic islands experiencing complete glaciation (Heard Island, South Georgia), these habitats are not currently thought to have survived glacial maxima, with increasing and compelling evidence for the extension of grounded ice sheets and shelves considerably deeper than those present today to the point of continental shelf drop-off (CLAPPERTON & SUGDEN 1982, 1988, LARTER & VANNESTE 1995, Ó COFAIGH et al. 2002). The integration of contemporary glaciological understanding and biogeographical evidence is, therefore, problematic, as no regional refugia are currently known (CONVEY 2003).

Recent and ongoing research is increasingly providing evidence pointing to the important contribution of ancient elements to the contemporary biota of Antarctica. Within the major taxonomic groups present in Antarctica, levels of endemism vary between the bryophytes, where virtually all Antarctic species have wider non-Antarctic distributions (PEAT et al. 2007), to the nematode worms, where according to some experts none are known outside Antarctica (ANDRÁSSY 1998 see CHOWN & CONVEY (2006, in press) for wider discussion of this topic). Within the Antarctic, some groups (nematodes, mites, springtails) show little or no overlap at species level between the maritime and continental Antarctic zones, to the extent that recognition of a major biogeographical divide has been proposed in the southern Antarctic Peninsula region (CHOWN & CONVEY, in press). Other groups (lichens, tardigrades) show intermediate levels of Antarctic endemism and overlap between Antarctic zones (ØVSTEDAL & SMITH 2001, CONVEY & MCINNES 2005). Lichens also provide an example of a group where evidence exists of the Antarctic continent being a source of propagules that can disperse northwards and colonise sites at lower latitudes. The observation that c. 40 % of the lichens of the isolated volcanic South Sandwich Islands archipelago are species otherwise known only from more southern Antarctic locations (CONVEY et al. 2000), combined with the recent age of these islands (0.5-3 Ma), indicates that an Antarctic source for these propagules must have existed over at least this timescale.

Providing a separate line of evidence, molecular biological approaches have demonstrated the processes of local population isolation and genetic radiation over at least the last million years in springtails from Victoria Land (continental Antarctica) (NOLAN et al. 2006, STEVENS & HOGG 2003, 2006A, 2006B, STEVENS et al. 2006, in press). The application of a “molecular clock” study to the phylogeny of some of the few Antarctic higher insects (chironomid midges, Diptera) has led to the proposal that these endemic species’ evolutionary lines have existed continuously on timescales of tens of millions of years on the tectonic sub-plates that together form the Antarctic Peninsula and Scotia Arc (ALLEGRUCCI et al. 2006), a timescale very consistent with the latest geological research into the timing of separation events leading to what is now the Drake Passage (LIVERMORE et al. 2005), but again highlighting the dichotomy between biological and glaciological data in this region.

PREDICTED CONSEQUENCES OF CLIMATE CHANGE FOR BIODIVERSITY

Antarctic terrestrial ecosystems, through their general simplicity of structure, are predicted to show particular sensitivity to, or recognisable consequences of, processes of environmental change (FRECKMAN & VIRGINIA 1997, BERGSTROM & CHOWN 1999, CONVEY 2003). One particular aspect of their simplicity that has excited some interest is that these ecosystems are likely to include examples where specific biological functional groups are not present or are poorly represented, and hence that there is little functional redundancy present. Thus, the redundancy achieved by having high species diversity within functional groups that is typical in more diverse lower latitude and tropical ecosystems is absent. In simple terms this means that in circumstances where change leads to the loss of an element of the Antarctic biota, their role may not simply be “taken over” by the flexibility of other members of the community, while where change leads to occupancy of a “new” niche becoming possible, there may not be taxa present locally with the ability to do so. In the first case, consequences at ecosystem level may be wide-ranging rather than restricted only to the directly impacted taxa. In the latter case, the community or ecosystem’s direct response to environmental change in situ becomes separated from responses involving long distance colonisation by taxa not currently present in the Antarctic biota. However, if or when such colonisation does take place, a separate fundamental characteristic of Antarctic terrestrial biota becomes highly significant – while the contemporary biota show many features of “adversity selection” (the ability to survive abiotic environmental extremes), competitive abilities are very poorly developed and communities and species are seen as vulnerable to increased competition, including predation, from invading taxa (CONVEY 1996b, 2003, FRENOT et al. 2005, CONVEY et al. 2006b). While over 200 non-indigenous species are already documented as having become established in Antarctica (FRENOT et al. 2005) (see below), the large majority of these relate to the sub-Antarctic islands. In these locations there are now many examples supporting the prediction of vulnerability of native biota to stronger competitors and predators. There are currently no analogous examples amongst the few species to have become established in the maritime and continental zones.

The two vascular plants native to the maritime Antarctic (*Deschampsia antarctica* and *Colobanthus quitensis*) have provided the most studied examples of measured biological response to recent environmental warming in this region (FOWBERT & SMITH 1994, SMITH 1994, GROBE et al. 1997, MCGRAW & DAY 1997, GERIGHAUSEN et al. 2003). Some local populations have increased by as much as two orders of magnitude in three decades, and there has been a change in the balance of reproductive strategy utilisation towards successful sexual reproduction (i.e. viable seed output) (CONVEY 1996c). Neither species has extended its southern distributional limit, although this is likely to be a function of a lack of suitable terrestrial habitat availability. More generally, the potential ecophysiological sensitivity of various Antarctic terrestrial biota to the different elements of environmental change is well recognised (e.g. SMITH 1999, KAPPEN 2000, CONVEY 2003, PANNEWITZ et al. 2005). However, still lacking in Antarctic biology are similar autecological studies identifying responses to recent environmental change by either the domi-

nant cryptogamic vegetation or non-manipulated whole communities (including both fauna and flora) in situ. BLOCK & CONVEY (2001) and CONVEY et al. (2003) have published data suggesting that elements of the maritime Antarctic microarthropod fauna are sensitive indicators of changes in patterns of water availability and, by implication, that biological responses to such changes will be expected.

In the absence of direct field observations, researchers have focused on the use of various long-term manipulation methodologies. While these have methodological weaknesses, such studies have found very rapid and large responses (biomass, morphology, numbers) in bryophytes, microbiota and fauna (SMITH 1993, 2001, KENNEDY 1994, WYNN-WILLIAMS 1996b, CONVEY & WYNN-WILLIAMS 2002) with greatly increased populations. Very few such studies have attempted to study responses at community level, or the effects of parallel manipulation of multiple environmental variables. An exception is provided by a detailed series of manipulations carried out near Anvers Island (maritime Antarctic) (DAY et al. 1999, 2001, CONVEY et al. 2002), which examined the consequences of manipulation of temperature, water and UV radiation at a range of levels from plant biochemistry and morphology to decomposition and the wider foodweb. Such studies illustrate an extremely important general biological point - biological responses to environmental change are generally unlikely to be “all or nothing”, rather being subtle and hard to detect. However, they are no less important through being subtle, as any response must require changes in resource allocation, and hence be involved in resource trade-offs with other elements of the life history. Very subtle changes within one organism at one trophic level can integrate through communities and ecosystems to become considerably more significant to other organisms (DAY 2001, SEARLES et al. 2001, CONVEY 2003).

THE MODERN DIMENSION – DIRECT HUMAN IMPACTS

While contemporary environmental changes, including both “global warming” and the separate process of stratospheric ozone depletion, are now clearly accepted as having a largely anthropogenic origin (KING 2005), they can be seen as examples of anthropogenic processes (i.e. pollution) having an indirect, though important, consequential impact on Antarctic biota. Antarctica also contains a signal of direct pollution reaching the continent through atmospheric transport (BARGAGLI 2005). It is also clear that human activity over the small number of centuries since the discoveries of the various Southern Ocean islands and the Antarctic continent has had various direct impacts on their terrestrial ecosystems, including their diversity and biogeography (FRENOT et al. 2005, CONVEY et al. 2006b, in press). These impacts on regional biogeography have taken place both through economic exploitation and the deliberate and accidental import and release of non-indigenous species. Most vulnerable to date are the sub-Antarctic islands where over 200 non-indigenous species (mostly vertebrates, arthropods, molluscs, vascular plants) are known already to be established. It is salient to note that several sub-Antarctic islands now host a greater diversity of non-indigenous higher plants than are present in their native flora. Much smaller numbers of introductions, as yet with restricted local distributions, are known from the maritime and

continental zones. As with the native biota of Antarctica, knowledge of the non-indigenous biota is at best patchy – vertebrates and vascular plants are relatively well documented, while knowledge of arthropods and other macro and microscopic invertebrates varies widely between locations depending on the availability of expertise. Cryptogams and, in particular, microbial groups have largely not been addressed (but see SJOLING & COWAN 2000, COWAN & AH TOW 2004, 2005). In that some level of introduction is unavoidable given that human activity in the Antarctic will continue (e.g. CHOWN & GASTON 2000), there is an urgent need for the establishment of baseline monitoring programmes (for a practical example see WHINAM et al. 2005) to enable the both the identification of future colonisation and introduction events, and the assessment of trends following introduction and establishment.

Some introductions clearly have had major and deleterious effects on sub-Antarctic ecosystems (reviewed by FRENOT et al. 2005, CONVEY et al. 2006b). For instance, the introduction of vertebrate herbivores and predators into ecosystems in which neither guild was represented has led to both considerable damage to and loss of habitat, and sometimes drastic reductions in populations of indigenous biota. While, not surprisingly, threats to native avifauna have received most attention to date, these consequences also spread to include elements of the invertebrate fauna. A number of vascular plants probably introduced amongst animal fodder have now become invasive and are displacing native flora from large areas of ecosystems. It is rapidly becoming clear that human activities pose probably the greatest contemporary threat to the biogeographical integrity of Antarctica, with species introductions via anthropogenic routes thought to outnumber “natural” colonisation events by two to three orders of magnitude (GASTON et al. 2003, FRENOT et al. 2005). This threat has largely yet to be realised on the Antarctic continent, but the experience already illustrated by the various sub-Antarctic islands provides a salient and clear warning of the consequences of any failure to respond, while the Antarctic Treaty System aims to encourage that the highest standards of environmental stewardship be applied to human activities in this region (DE POORTER et al. 2006).

CONCLUSIONS

While it is indisputable that rates of contemporary environmental change in parts of Antarctica are among the most rapid seen anywhere on the planet, it is also the case that many Antarctic terrestrial organisms already possess features that mean they are well adapted to their stressful and very variable environment (CONVEY 1996b). In this context, even in the Antarctic, observed and predicted levels of anthropogenic change are often small compared with natural scales of variation. Therefore, it appears that these organisms will often benefit from reduced environmental stress (particularly through warming and/or greater water availability), as this will reduce the requirement to invest resources in expensive stress tolerance tactics, while permitting faster growth rates leading to shorter life cycles and population increases (CONVEY 2003, 2006). It is obviously also the case that negative consequences may be seen at local scale, for instance associated with reduced water input, interactions between warming and drying, and areas where radiation damage can be shown to

increase. Indeed, rather than being threatened directly by climate change, the greatest threat to Antarctic terrestrial biota and ecosystems comes in the form of vulnerability to colonisation and invasion by non-indigenous species. While Antarctica has in general been protected from such species and invasions (from natural or anthropogenic sources) by its remoteness, it now faces the twin challenges of environmental change, which reduces the hurdles to be overcome during colonisation and establishment, and deliberate and accidental human import of non-indigenous species.

ACKNOWLEDGMENTS

The author thanks the organisers of the 22nd International Meeting of the German Society for Polar Research for the opportunity to participate in the symposium that led to this paper. Prof. L. Kappen and an anonymous reviewer are thanked for their helpful comments on an earlier version of the manuscript. Katrin Linse kindly provided translations for the Abstract and captions. The paper forms a contribution to the BAS “BIOPEARL” project and the SCAR “Evolution and Biodiversity in Antarctica” programme. Figure 1 is reproduced with the permission of Blackwell Publishing.

References

- Adams, B., Bardgett, R.D., Ayres, E., Wall, D.H., Aislabie, J., Bamforth, S., Bargagli, R., Cary, C., Cavacini, P., Connell, L., Convey, P., Fell, J., Frati, F., Hogg, I., Newsham, N., O'Donnell, A., Russell, N., Seppelt, R. & Stevens, M.I. (2006): Diversity and distribution of Victoria Land biota.- *Soil Biol. Biochem.* 38: 3003-3018.
- Allegrucci, G., Carchini, G., Todisco, V., Convey, P. & Sbordoni, V. (2006): A molecular phylogeny of Antarctic Chironomidae and its implications for biogeographical history.- *Polar Biol.* 29: 320-326.
- Andrássy, I. (1998): Nematodes in the sixth continent.- *J. Nematode Morphol. Syst.* 1: 107-186.
- Bargagli, R. (2005). Antarctic ecosystems.- *Ecological Studies Series 175*, Springer, Berlin, 1-395.
- Barnes, D.K.A., Hodgson, D.A., Convey, P., Allen, C. & Clarke, A. (2006): Incursion and excursion of Antarctic biota: past, present and future.- *Glob. Ecol. Biogeogr.* 15: 121-142.
- Bergstrom, D.M. & Chown, S.L. (1999): Life at the front: history, ecology and change on southern ocean islands.- *Trends Ecol. Evol.* 14: 472-476.
- Bergstrom, D., Hodgson, D.A. & Convey, P. (in press): The physical setting of the Antarctic.- In: D.M. BERGSTROM, P. CONVEY & A.H.L. HUISKES (eds), *Trends in Antarctic terrestrial and limnetic ecosystems*, Springer, Dordrecht.
- Beyer, L. & Bölter, M. (eds) (2002): *Geocology of Antarctic ice-free coastal landscapes.- Ecological Studies Series 154*, Springer, Berlin, XXIV, 1-427.
- Björk, S., Malmer, N., Sandgren, P., Ingólfsson, O., Wallén, B., Smith, R.I.L. & Jónsson, B.L. (1991): Stratigraphic and paleoclimatic studies of a 5500-year-old moss bank on Elephant Island, Antarctica.- *Arct. Alpine Res.* 23: 361-374.
- Block, W. (1984): Terrestrial microbiology, invertebrates and ecosystems.- In: R.M. LAWS (ed), *Antarctic ecology*, Academic Press, London, 163-236.
- Block, W. (1996): Cold or drought - the lesser of two evils for terrestrial arthropods? - *Eur. J. Entomol.* 93: 325-339.
- Block, W. & Convey, P. (2001): Seasonal and long-term variation in body water content of an Antarctic springtail - a response to climate change? - *Polar Biol.* 24: 764-770.
- Boenigk, J., Pfandl, K., Garstecki, T., Harms, H., Novarino, G. & Chatzinotas, A. (2006): Evidence for geographic isolation and signs of endemism within a protistan morphospecies.- *Appl. Environm. Microbiol.* 72: 5159-5164.
- Boyer, S.J. (1979): Glacial geologic observations in the Dufek Massif and Forrester Range, 1978-79.- *Antarct. J. US* 14: 46-48.
- Brinkmann, M., Pearce, D.A., Convey, P. & Ott, S. (in press): The cyanobacterial community of polygon soils at an Antarctic terrestrial inland site – Coal Nunatak, Alexander Island.- *Polar Biology*.
- BAS (2004): Antarctica 1:10,000,000 map. - BAS (misc) 11, British Antarctic

- Survey, Cambridge.
- Broadly, P.A. (1996): Diversity, distribution and dispersal of Antarctic terrestrial algae.- *Biodiversity and Conservation* 5: 307-335.
- Budd, W.F. & Simmonds, L. (1991): The impact of global warming on the Antarctic mass balance and global sea level.- In: G. WELLER, C.L. WILSON & B.A.B. SEVERIN (eds), Proceedings of the international conference on the role of polar regions in global change, Geophys. Inst. Univ. Alaska, Fairbanks, 489-494.
- Chapuis, J.L., Frenot, Y. & Lebouvier, M. (2004): Recovery of native plant communities after eradication of rabbits from the subantarctic Iles Kerguelen, and influence of climate change.- *Biol. Conserv.* 117: 167-179.
- Chown, S.L. & Convey, P. (2006 in press): Biogeography.- In: D.M. BERGSTROM, P. CONVEY & A.H.L. HUISKES (eds), Trends in Antarctic terrestrial and limnetic ecosystems, Springer, Dordrecht.
- Chown, S.L. & Convey, P. (in press): Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic.- *Phil. Trans. Roy. Soc. Lond. Ser. B*.
- Chown, S.L. & Gaston, K.J. (2000): Island hopping invaders hitch a ride with tourists in the Southern Ocean.- *Nature* 408: 637.
- Chown, S.L., Gremen, N.J.M. & Gaston, K.J. (1998): Ecological biogeography of the Southern Ocean Islands: species-area relationships, human impacts, and conservation.- *Amer. Nat.* 152: 562-575.
- Christner, C., Kvitko, B.H. & Reeve, J.N. (2003): Molecular identification of bacteria and eukarya inhabiting an Antarctic cryoconite hole.- *Extremophiles* 7: 177-183.
- Clapperton, C.M. & Sugden, D.E. (1982): Late Quaternary glacial history of George VI Sound area, West Antarctica.- *Quatern. Res.* 18: 243-267.
- Clapperton, C.M. & Sugden, D.E. (1988): Holocene glacier fluctuations in South America and Antarctica.- *Quatern. Sci. Rev.* 7: 185-198.
- Clarke, A. (2003): Evolution, adaptation and diversity: global ecology in an Antarctic context.- In: A.H.L. HUISKES, W.W.C. GIESKES, J. ROZEMA, R.M.L. SCHORNO, S.M. VAN DER VRIES & W.J. WOLFF (eds), Antarctic biology in a global context, Backhuys, Leiden, 3-17.
- Clarke, A., Barnes, D.K.A. & Hodgson, D.A. (2005): How isolated is Antarctica? - *Trends Ecol. Evol.* 20: 1-3.
- Clarke, A. & Crame, J.A. (1989): The origin of the Southern Ocean marine fauna.- In: J.A. Crame (ed), Origins and evolution of the Antarctic biota, Geol. Soc. London, 253-268.
- Convey, P. (1996a): Overwintering strategies of terrestrial invertebrates in Antarctica - the significance of flexibility in extremely seasonal environments.- *Eur. J. Entomol.* 93: 489-505.
- Convey, P. (1996b): The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota.- *Biol. Rev.* 71, 191-225.
- Convey, P. (1996c): Reproduction of Antarctic flowering plants.- *Antarct. Sci.* 8: 127-134.
- Convey, P. (2001): Antarctic Ecosystems.- In: S.A. LEVIN (ed), Encyclopedia of biodiversity, 1st Edition, Academic Press, San Diego, Vol. 1: 171-184.
- Convey, P. (2003): Maritime Antarctic climate change: signals from terrestrial biology.- *Antarct. Res. Ser.* 79: 145-158.
- Convey, P. (2006 in press): Antarctic climate change and its impacts on terrestrial ecosystems.- In: D.M. BERGSTROM, P. CONVEY & A.H.L. HUISKES (eds), Trends in Antarctic terrestrial and limnetic ecosystems, Springer, Dordrecht.
- Convey, P. (in press): Antarctic Ecosystems.- In: S.A. LEVIN (ed), Encyclopedia of biodiversity, 2nd Edition, Elsevier, San Diego.
- Convey, P., Barnes, D.K.A., Clark, M.S., Dominic A., Hodgson, D.A. & Peck, L.S. (in press): An holistic approach to understanding the biological impacts of climate change: Antarctica as a planetary warning system.- *Inside Agric.*
- Convey, P., Block, W. & Peat, H.J. (2003): Soil arthropods as indicators of water stress in Antarctic terrestrial habitats? - *Global Change Biol.* 9: 1718-1730.
- Convey, P., Chown, S.L., Wasley, J. & Bergstrom, D.M. (2006a in press): Life history traits.- In: D.M. BERGSTROM, P. CONVEY & A.H.L. HUISKES (eds), Trends in Antarctic terrestrial and limnetic ecosystems, Springer, Dordrecht.
- Convey, P., Frenot, Y., Gremen, N. & Bergstrom, D. (2006b in press): Antarctic invasions.- In: D.M. BERGSTROM, P. CONVEY & A.H.L. HUISKES (eds), Trends in Antarctic terrestrial and limnetic Ecosystems, Springer, Dordrecht.
- Convey, P. & McInnes, S.J. (2005): Exceptional, tardigrade dominated, ecosystems from Ellsworth Land, Antarctica.- *Ecology* 86: 519-527.
- Convey, P., Pugh, P.J.A., Jackson, C., Murray, A.W., Ruhland, C.T., Xiong, F.S. & Day, T.A. (2002): Response of Antarctic terrestrial arthropods to multifactorial climate manipulation over a four year period.- *Ecology* 83: 3130-3140.
- Convey, P., Smith, R.I.L., Hodgson, D.A. & Peat, H.J. (2000): The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating.- *J. Biogeogr.* 27: 1279-1295.
- Convey, P. & Wynn-Williams, D.D. (2002): Antarctic soil nematode response to artificial environmental manipulation.- *Eur. J. Soil Biol.* 38: 255-259.
- Cowan, D.A. & Ah Tow, L. (2004): Endangered Antarctic microbial communities.- *Ann. Rev. Microbiol.* 58: 649-690.
- Cowan, D.A. & Ah Tow, L. (2005): Dissemination and survival of non-indigenous bacterial genomes in pristine Antarctic environments.- *Extremophiles* 9: 385-389.
- Cullather, R.I., Bromwich, D.H. & van Woert, M.L. (1996): Inter-annual variations in Antarctic precipitation related to El Niño - Southern Oscillation.- *J. Geophys. Res.* 101: 19109-19118.
- Danks, H.V. (1999): Life cycles in polar arthropods - flexible or programmed? - *Eur. J. Entomol.* 96: 83-102.
- Day, T.A. (2001): Multiple trophic levels in UV-B assessments - completing the ecosystem.- *New Phytol.* 152: 183-186.
- Day, T.A., Ruhland, C.T. & Xiong, F. (2001): Influence of solar UV-B radiation on Antarctic terrestrial plants: results from a 4-year field study.- *J. Photochem. Photobiol. B: Biol.* 62: 78-87.
- Day, T.A., Ruhland, C.T., Grobe, C.W. & Xiong, F. (1999): Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field.- *Oecologia* 119: 24-35.
- De Poorter, M., Gilbert, N., Storey, B. & Rogan-Finnemore, M. (2006): Non-native species in the Antarctic, a workshop. Final Report, Gateway Antarctica, Christchurch, 1-40.
- EPICA (2004): Eight glacial cycles from an Antarctic ice core.- *Nature* 429: 623-628.
- Farman, J.C., Gardiner, B.G. & Shanklin, J.D. (1985): Large losses of total ozone in Antarctica reveal seasonal ClOx/NOx interaction.- *Nature* 315: 207-210.
- Fenton, J.H.C. & Smith, R.I.L. (1982): Distribution, composition and general characteristics of the moss banks of the maritime Antarctic.- *Brit. Antarct. Surv. Bull.* 51: 215-236.
- Finlay, B.J. (2002): Global dispersal of free-living microbial eukaryote species.- *Science* 296: 1061-1063.
- Fowbert, J.A. & Smith, R.I.L. (1994): Rapid population increase in native vascular plants in the Argentine Islands, Antarctic Peninsula.- *Arct. Alpine Res.* 26: 290-296.
- Franzmann, P.D. (1996): Examination of Antarctic prokaryotic diversity through molecular comparisons.- *Biodiversity and Conservation* 5: 1295-1305.
- Freckman, D.W. & Virginia, R.A. (1997): Low-diversity Antarctic soil nematode communities: distribution and response to disturbance.- *Ecology* 78: 363-369.
- Friedmann, E.I. (1982): Endolithic microorganisms in the Antarctic cold desert.- *Science* 215: 1045-1053.
- Frenot, Y., Gloguen, J.-C. & Trehen, P. (1997): Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa kerguelensis* and *P. annua*.- In: B. BATTAGLIA, J. VALENCIA & D.W.H. WALTON (eds), Antarctic communities: species, structure and survival, Cambridge University Press, Cambridge, 358-366.
- Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P., Convey, P., Skotnicki, M. & Bergstrom, D. (2005): Biological invasions in the Antarctic: extent, impacts and implications.- *Biol. Rev.* 80: 45-72.
- Gaston K.J., Jones A.G., Hänel, C. & Chown S.L. (2003): Rates of species introduction to a remote oceanic island.- *Proc. Roy. Soc. London B* 270: 1091-1098.
- Gerighausen, U., Bräutigam, K., Mustafa, O. & Peter, H.-U. (2003): Expansion of vascular plants on an Antarctic island - a consequence of climate change? - In: A.H.L. HUISKES, W.W.C. GIESKES, J. ROZEMA, R.M.L. SCHORNO, S.M. VAN DER VRIES & W.J. WOLFF (eds), Antarctic biology in a global context, Backhuys, Leiden, 79-83.
- Greenslade, P. (2006): The invertebrates of Macquarie Island.- *Australian Antarctic Division, Kingston, Tasmania*, xvi, 1-326.
- Grobe, C.W., Ruhland C.T. & Day, T.A. (1997): A new population of *Colobanthus quitensis* near Arthur Harbor, Antarctica: correlating recruitment with warmer summer temperatures.- *Arct. Alpine Res.* 29: 217-221.
- Gressitt, J.L. (1965): Biogeography and ecology of land arthropods of Antarctica.- In: J. VAN MIEGHEM, P. VAN OYE & J. SCHELL (eds), Biogeography and ecology in Antarctica, Junk, The Hague, 431-490.
- Gressitt, J.L. (1970): Subantarctic entomology and biogeography.- *Pac. Insects Monogr.* 23: 295-374.
- Gressitt, J.L. (1971): Antarctic entomology with emphasis on biogeographical aspects.- *Pac. Insects Monogr.* 25: 167-178.
- Gressitt, J.L., Larch, R.E. & O'Brien, C.W. (1960): Trapping air-borne insects in the Antarctic area.- *Pac. Insects* 2: 245-250.
- Harangozo, S.A. (2000): A search for ENSO teleconnections in the west Antarctic Peninsula climate in austral winter.- *Int. J. Climatol.* 20: 663-679.
- Hjort, C., Ingólfsson, Ó., Bentley, M.J. & Björck, S. (2003): The late Pleistocene and Holocene glacial and climate history of the Antarctic Peninsula region as documented by the land and lake sediment records - a review.- *Antarct. Res. Ser.* 79: 95-102.
- Hodgson, D.A., Roberts, D., McMinn, A., Verleyen, E., Terry, B., Corbett, C. & Vyverman, W. (2006): Recent rapid salinity rise in three East Antarctic lakes.- *J. Paleolimnol.* DOI 10.1007/s10933-006-9010-0

- Hogg, I.D., Cary, S.C., Convey, P., Newsham, K.K., O'Donnell, T., Adams, B.J., Aislabie, J., Frati, F.F., Stevens, M.I. & Wall, D.H. (2006): Biotic interactions in Antarctic terrestrial ecosystems: are they a factor? - *Soil Biol. Biochem.* 38: 3035-3040.
- Hughes, K.A. & Lawley, B. (2003): A novel Antarctic microbial endolithic community within gypsum crusts. - *Environm. Microbiol.* 5: 555-565.
- Hughes, K.A., McCartney, H.A., Lachlan-Cope, T.A. & Pearce D.A. (2004): A preliminary study of airborne microbial biodiversity over peninsular Antarctica. - *Cell. Molec. Biol.* 50: 537-542.
- Jacka, T.H. & Budd, W.F. (1998): Detection of temperature and sea-ice-extent changes in the Antarctic and Southern Ocean, 1949-96. - *Annals. Glaciol.* 27: 553-559.
- Kappen, L. (2000): Some aspects of the great success of lichens in Antarctica. - *Antarct. Sci.* 12: 314-324.
- Kennedy, A.D. (1993): Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. - *Arct. Alpine Res.* 25: 308-315.
- Kennedy, A.D. (1994): Simulated climate change: a field manipulation study of polar microarthropod community response to global warming. - *Ecography* 17: 131-140.
- King, D. (2005): Climate change: the science and the policy. - *J. Appl. Ecol.* 42: 779-783.
- King, J.C., Turner, J., Marshall, G.J., Conolley W.M. & Lachlan-Cope, T.A. (2003): Antarctic Peninsula climate variability and its causes as revealed by analysis of instrumental records. - *Antarct. Res. Ser.* 79: 17-30.
- Larter, R.D. & Vanneste, L.E. (1995): Relict subglacial deltas on the Antarctic Peninsula outer shelf. - *Geology* 23: 33-36.
- Lawley, B., Ripley, S., Bridge, P. & Convey, P. (2004): Molecular analysis of geographic patterns of eukaryotic diversity in Antarctic soils. - *Appl. Environm. Microbiol.* 70: 5963-5972.
- Leather, S.R., Walters, K.F.A. & Bale, J.S. (1993): The ecology of insect overwintering. - Cambridge University Press, Cambridge, 1-255.
- Lister, A., Block, W. & Usher, M.B. (1988): Arthropod predation in an Antarctic terrestrial community. - *J. Anim. Ecol.* 57: 957-971.
- Livermore, R.A., Nankivell, A.P., Eagles, G. & Morris, P. (2005): Paleogene opening of Drake Passage. - *Earth Planet. Sci. Lett.* 236: 459-470.
- Longton, R.E. (1988): Biology of polar bryophytes and lichens. - Cambridge University Press, Cambridge, VIII, 1-391.
- Lorius, C., Jouzel, J., Ritz, C., Merlivat, L. & Barkov, N.I. (1985): A 150,000-year climate record from Antarctic ice. - *Nature* 316: 591-596.
- Lyons, W.B., Howard-Williams, C. & Hawes, I. (eds) (1997): Ecosystem processes in Antarctic ice-free landscapes. - Balkema, Rotterdam, XII, 1-281.
- Marshall, D.J. & 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. - *Zool. J. Linn. Soc.* 129: 111-128.
- Marshall, D.J. & Pugh, P.J.A. (1996): Origin of the inland Acari of continental Antarctica, with particular reference to Dronning Maud Land. - *Zool. J. Linn. Soc.* 118: 101-118.
- Marshall, W.A. (1996): Biological particles over Antarctica. - *Nature* 383: 680.
- Maslen, N.R. & Convey, P. (2006): Nematode diversity and distribution in the southern maritime Antarctic – clues to history? - *Soil Biol. Biochem.* 38: 3141-3151.
- McGraw, J.B. & Day, T.A. (1997): Size and characteristics of a natural seed bank in Antarctica. - *Arct. Alpine Res.* 29: 213-216.
- Mitchell A.D., Meurk, C.D. & Wagstaff, S.J. (1999): Evolution of *Stilbocarpa*, a megaherb from New Zealand's sub-Antarctic islands. - *NZ J. Botany* 37: 205-211.
- Mueller, D.R. & Pollard, W.H. (2004): Gradient analysis of cryoconite ecosystems from two polar glaciers. - *Polar Biol.* 27: 66-74.
- Muñoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. & 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. & Haase, M. (2006): Fine scale distribution of mtDNA haplotypes for the springtail *Gomphiocephalus hodgsoni* (Collembola) corresponds to an ancient shoreline in Taylor Valley, continental Antarctica. - *Polar Biol.* DOI 10.1007/s00300-006-0119-4.
- Noon, P.E., Birks, H.J.B., Jones, V.J. & Ellis-Evans, J.C. (2001): Quantitative models for reconstructing catchment ice-extent using physical-chemical characteristics of lake sediments. - *J. Palaeolimnol.* 25: 375-392.
- Ó Cofaigh, C., Pudsey, C.J., Dowdeswell, J.A., & Morris, P. (2002): Evolution of subglacial bedforms along a paleo-ice stream, Antarctic Peninsula continental shelf. - *Geophys. Res. Lett.* 29: 10.1029/2001.GL014488.
- Øvstedal, D.O. & Smith, R.I.L. (2001): Lichens of Antarctica and South Georgia. A guide to their identification and ecology, Cambridge University Press, Cambridge, XII, 1-411.
- Pannewitz, S., Green, T.G.A., Maysek, K., Schlenso, M., Seppelt, R., Sancho, L.G., Türk, R. & Schroeter, B. (2005): Photosynthetic responses of three common mosses from continental Antarctica. - *Antarct. Sci.* 17: 341-352.
- Peat, H.J., Clarke, A. & Convey, P. (2007): Diversity and biogeography of the Antarctic flora. - *J. Biogeogr.* 34: 132-146.
- Peck, L.S., Convey, P. & Barnes, D.K.A. (2006): Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. - *Biol. Rev.* 81: 75-109.
- Pegler, D.N., Spooner, B.M. & Smith, R.I.L. (1980): Higher fungi of Antarctica, the subantarctic zone and Falkland Islands. - *Kew Bull.* 35: 499-562.
- Poole, I. & Cantrill, D. (2001) Fossil woods from Williams Point beds, Livingston Island, Antarctica: a late Cretaceous southern high latitude flora. - *Palaeontology* 44: 1081-1112.
- Prentice, M.L., Bockheim, J.G., Wilson, S.C., Burckle, L.H., Hodell, D.A., Schlichter, C. & Kellogg, D.E. (1993): Late Neogene Antarctic glacial history: evidence from central Wright Valley. - *Antarct. Res. Ser.* 60: 207-250.
- Pudsey, C.J. & Evans, J. (2001): First survey of Antarctic sub-ice shelf sediments reveals mid-Holocene ice shelf retreat. - *Geology* 29: 787-790.
- van der Putten, N. & Verbruggen, C. (2005): The onset of deglaciation of Cumberland Bay and Stromness Bay, South Georgia. - *Antarct. Sci.* 17: 29-32.
- Quayle, W.C., Convey, P., Peck, L.S., Ellis-Evans, J.C., Butler, H.G. & Peat, H.J. (2003): Ecological responses of maritime Antarctic lakes to regional climate change. - *Antarct. Res. Ser.* 79: 159-170.
- Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C. & Harrigan, P.R. (2002): Extreme responses to climate change in Antarctic lakes. - *Science* 295: 645.
- Rønning, O.I. (1996): The flora of Svalbard, Norsk Polarinstut, Oslo, 1-184.
- Rozema, J. (ed) (1999): Stratospheric ozone depletion, the effects of enhanced UV-B radiation on terrestrial ecosystems, Backhuys, Leiden, VII, 1-355.
- Santas, R., Koussoulaki, A. & Häder, D.-P. (1997): In assessing biological UV-B effects, natural fluctuations of solar radiation should be taken into account. - *Plant Ecol.* 128: 93-97.
- Schlenso, M., Pannewitz, S., Green, T.G.A. & Schroeter, B. (2004): Metabolic recovery of continental antarctic cryptogams after winter. - *Polar Biol* 27: 399-408.
- Searles, P.S., Kropp, B.R., Flint, S.D. & Caldwell, M.M. (2001): Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. - *New Phytol.* 152: 213-221.
- Selmi, S. & Boulinier, T. (2001): Ecological biogeography of southern ocean islands: the importance of considering spatial issues. - *Amer. Nat.* 158: 426-437.
- Sjoling, S. & Cowan, D.A. (2000): Presence of human-specific enteric microorganisms in current and historic field camp sites. - *Polar Biol.* 23: 644-650.
- Smith R.I.L. (1984): Terrestrial plant biology of the Sub-Antarctic and Antarctic. - In: R.M. LAWS (ed), Antarctic ecology, Academic Press, London, 61-162.
- Smith, R.I.L. (1990): Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. - In: K.R. KERRY & G. HEMPEL (eds), Antarctic ecosystems, ecological change and conservation, Springer-Verlag, Berlin, 32-50.
- Smith, R.I.L. (1993): The role of bryophyte propagule banks in primary succession: case study of an Antarctic fellfield soil. - In: J. MILES & D.W.H. WALTON (eds), Primary succession on land, Blackwell, Oxford, 55-78.
- Smith, R.I.L. (1994): Vascular plants as indicators of regional warming in Antarctica. - *Oecologia* 99: 322-328.
- Smith, R.I.L. (1999): Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. - *J. Veg. Res.* 10: 231-242.
- Smith, R.I.L. (2001): Plant colonization response to climate change in the Antarctic. - *Folia Fac. Sci. Nat. Univ. Masarykianae Brunensis, Geographia* 25: 19-33.
- Smith, V.R. (2002): Climate change in the sub-Antarctic: an illustration from Marion Island. - *Climate Change* 52: 345-357.
- Smith, V.R. & Steenkamp, M. (1990): Climatic change and its ecological implications at a sub-Antarctic island. - *Oecologia* 85: 14-24.
- Somme, L. (1986): Ecology of *Cryptopygus sverdrupi* (Insecta: Collembola) from Dronning Maud Land, Antarctica. - *Polar Biol.* 6: 179-184.
- Somme, L. (1995): Invertebrates in hot and cold arid environments, Springer-Verlag, Berlin, XIV, 1-275.
- Stevens, M.I. & 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. - *Molec. Ecol.* 12: 2357-2369.
- Stevens, M.I. & Hogg, I.D. (2006a in press): The molecular ecology of Antarctic terrestrial and limnetic invertebrates and microbes. - In: D.M. BERGSTROM, P. CONVEY & A.H.L. HUIKES (eds), Trends in Antarctic terrestrial and limnetic ecosystems, Springer, Dordrecht.
- Stevens, M.I. & Hogg, I.D. (2006b): Contrasting levels of mitochondrial DNA variability between mites (Penthaloudidae) and springtails (Hypogastruridae) from the Trans-Antarctic Mountains suggest long-term effects of glaciation and life history on substitution rates, and speciation processes. - *Soil Biol. Biochem.* 38: 3171-3180.
- Stevens, M.I., Greenslade, P., Hogg, I.D. & Sunnucks, P. (2006): Southern

- hemisphere springtails: could any have survived glaciation of Antarctica? - *Molec. Biol. Evol.* 23: 874-882.
- Stevens, M.I., Frati, F., McGaughran, A., Spinsanti, G. & Hogg, I.D.* (in press): Phylogeographic structure suggests multiple glacial refugia in northern Victorian Land for the endemic springtail *Desoria klovstadi* (Collembola, Isotomidae). - *Zoologica Scripta*.
- Turner, J., Colwell, S.R. & Harangozo, S.* (1997): Variability of precipitation over the coastal western Antarctic Peninsula from synoptic observations. - *J. Geophys. Res.* 102: 13999-14007.
- Tweedie, C.E. & Bergstrom, D.M.* (2000): A climate change scenario for surface air temperature at subantarctic Macquarie Island. - In: W. DAVISON, C. HOWARD-WILLIAMS & P.A. BROADY (eds), *Antarctic ecosystems: models for wider ecological understanding*, New Zealand Nat. Sci., Christchurch, 272-281.
- Usher, M.B., Block, W. & Jumeau, P.J.A.M.* (1989): Predation by arthropods in an Antarctic terrestrial community. - In: R.B. HEYWOOD (ed), *University research in Antarctica (Antarctic special topic)*, British Antarctic Survey, Cambridge, 123-129.
- Vaughan, D.G.* (2006): Trends in melting conditions on the Antarctic Peninsula and their implications for ice sheet mass balance. - *Arct. Antarct. Alpine Res.* 38: 147-152.
- Vaughan, D.G., Marshall, G.J., Connolley, W.C., King, J.C. & Mulvaney, R.* (2001): Devil in the detail - *Science* 293: 1777-1779.
- Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C.L., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J. & Turner, J.* (2003): Recent rapid regional climate warming on the Antarctic Peninsula. - *Climate Change* 60: 243-274.
- Vincent, W.F.* (1988): *Microbial ecosystems of Antarctica*. - Cambridge University Press, Cambridge, XIV, 1-304.
- Vishniac, H.S.* (1996): Biodiversity of yeasts and filamentous microfungi in terrestrial Antarctic ecosystems. - *Biodivers. Conserv.* 5: 1365-1378.
- Whinam, J., Chilcott N. & Bergstrom D.M.* (2004): Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. - *Biol. Conserv.* 121: 207-219.
- Wynn-Williams, D.D.* (1993): Microbial processes and the initial stabilisation of fellfield soil. - In: J. MILES & D.W.H. WALTON (eds), *Primary succession on land*, Blackwell, Oxford, 17-32.
- Wynn-Williams, D.D.* (1996a): Antarctic microbial diversity: the basis of polar ecosystem processes. - *Biodivers. Conserv.* 5: 1271-1293.
- Wynn-Williams, D.D.* (1996b): Response of pioneer soil microalgal colonists to environmental change in Antarctica. - *Microbiol. Ecol.* 31: 177-188.
- Yergeau, E., Bokhorst, S., Huiskes, A.H.L., Boschker, H.T.S., Aerts, R. & Kowalchuk, G.A.* (2006): Size and structure of bacterial, fungal and nematode communities along an Antarctic environmental gradient. - *FEMS Microbiol. Ecol.* DOI:10.1111/j.1574-6941.2006.00200.x.