

# Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic

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Antarctica and its surrounding islands lie at one extreme of global variation in diversity. Typically, these regions are characterized as being species poor and having simple food webs. Here, we show that terrestrial systems in the region are nonetheless characterized by substantial spatial and temporal variations at virtually all of the levels of the genealogical and ecological hierarchies which have been thoroughly investigated. Spatial variation at the individual and population levels has been documented in a variety of genetic studies, and in mosses it appears that UV-B radiation might be responsible for within-clump mutagenesis. At the species level, modern molecular methods have revealed considerable endemism of the Antarctic biota, questioning ideas that small organisms are likely to be ubiquitous and the taxa to which they belong species poor. At the biogeographic level, much of the relatively small ice-free area of Antarctica remains unsurveyed making analyses difficult. Nonetheless, it is clear that a major biogeographic discontinuity separates the Antarctic Peninsula and continental Antarctica, here named the 'Gressitt Line'. Across the Southern Ocean islands, patterns are clearer, and energy availability is an important correlate of indigenous and exotic species richness, while human visitor numbers explain much of the variation in the latter too. Temporal variation at the individual level has much to do with phenotypic plasticity, and considerable life-history and physiological plasticity seems to be a characteristic of Antarctic terrestrial species. Environmental unpredictability is an important driver of this trait and has significantly influenced life histories across the region and probably throughout much of the temperate Southern Hemisphere. Rapid climate change-related alterations in the range and abundance of several Antarctic and sub-Antarctic populations have taken place over the past several decades. In many sub-Antarctic locations, these have been exacerbated by direct and indirect effects of invasive alien species. Interactions between climate change and invasion seem set to become one of the most significant conservation problems in the Antarctic. We conclude that despite the substantial body of work on the terrestrial biodiversity of the Antarctic, investigations of interactions between hierarchical levels remain scarce. Moreover, little of the available information is being integrated into terrestrial conservation planning, which lags far behind in this region by comparison with most others.

**Keywords:** biogeography; biological invasions; climate change; conservation planning; extinction; phenotypic plasticity

## 1. INTRODUCTION

Of all the characteristics of biodiversity, the most noteworthy is its variability. Recognition that the significance of the mechanisms underlying this variation changes as the scale of interest is altered, and that variation at one level may cascade up (or down) to affect many others in the ecological and genealogical hierarchies, are hallmarks of modern ecology (Wiens 1989). For example, it is clear that both local and regional scale processes affect the identity and richness of species at any given site (Ricklefs 1987, 2004; Hawkins & Porter 2003; Witman *et al.* 2004) and that local-regional interactions can profoundly affect the properties of assemblages (Gaston 2000; Blackburn & Gaston 2001a;

Leibold *et al.* 2004; Rangel & Diniz-Filho 2005), even in circumstances where life-history characteristics have little influence over the demographic rates of their constituent species (Hubbell 2001; He 2005). Likewise, genetic-level variation in primary producers can cascade up through individuals to affect the functioning of whole ecosystems, including feedback loops to plant performance (Treseder & Vitousek 2001; Whitham *et al.* 2003). In consequence, understanding the determinants of biodiversity requires investigation of processes at a variety of spatial and temporal scales, and as a first step, the identification of the patterns which are the reflection, though sometimes beguiling, of these processes (Gaston & Blackburn 1999). Doing so is essential not only because of the insight into the natural world that such understanding brings, but also because it is only in this way that appropriate interventions can be recommended to slow the extraordinary impact humans are having on regional and global diversities

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(Brooks *et al.* 2002; Thomas *et al.* 2004; Balmford *et al.* 2005; Gaston 2005).

In the terrestrial ecosystems of the Antarctic (including the outlying sub-Antarctic islands), these impacts are smaller than they have been elsewhere. Humans first sighted the Antarctic Peninsula in 1820, with the first landing probably in 1821, and the first landing on East Antarctica (at Cape Adare) in 1895. Many of the sub-Antarctic islands have equally short human histories (Headland 1989; Chown *et al.* 2005). Early human impacts were mostly restricted to marine systems as a consequence of sealing and whaling (Knox 1994), with changes to the terrestrial environment being localized in their extent and nature. Now, the situation is quite different, and both the direct local and indirect influences of humans are increasing across the region. For example, invasive alien species have profoundly altered species assemblages and ecosystem functioning on most sub-Antarctic islands, and their direct effects are starting to be felt on the continent itself (Frenot *et al.* 2005), often in ways that are not immediately obvious (Kerry 1990; Wynn-Williams 1996; Hughes 2003). Indirect human influences include the long-range transport to and the presence of persistent organic and inorganic pollutants in Antarctic systems (Corsolini *et al.* 2002; Bargagli 2005; Dickhut *et al.* 2005), and the substantial alterations to terrestrial communities as a consequence of changing climates associated with global warming (Lewis Smith 1994; Bergstrom & Chown 1999; Walther *et al.* 2002; Convey 2003a). The significance of these impacts, and their scope for increase, given ongoing global change (Watson 2002) and growing human use of the Antarctic (Naveen *et al.* 2001; Frenot *et al.* 2005), have been recognized by the Committee for Environmental Protection of the Antarctic Treaty System, and by those nations that have responsibility for the sub-Antarctic islands (e.g. Anonymous 1996; McIntosh & Walton 2000). Both the requirements for conservation of Antarctic systems and the ways in which the probable impacts of increasing human travel to the Antarctic can be mitigated are major issues of political concern (<http://www.cep.ats.aq/cep/>). However, these issues can only be adequately addressed with a sound understanding of the spatial and temporal variability of Antarctic terrestrial biodiversity, the processes underlying it, and the ways in which humans are currently affecting Antarctic environments and are likely to do so in the future.

Antarctic terrestrial diversity lies at the low end of the global spectrum for many, if not most organisms (Convey 2001; Clarke 2003), food webs are typically simple (Block 1984, 1985, 1994; Burger 1985; Freckman & Virginia 1997; Wall & Virginia 1999), and life histories tend to be dominated by responses to a seasonally variable, 'stressful' environment (Lewis Smith 1984; Convey 1996a; Vernon *et al.* 1998). Moreover, very little of the largely ice-covered Antarctic continent (0.32% ice-free, British Antarctic survey 2004) is available to the terrestrial biota. Even in the areas that can be used, substantial spatial variation in abundance and occupancy exists (Janetschek 1970; Lewis Smith 1984; Kennedy 1993). Indeed, it has been clear ever since extensive work on Antarctic terrestrial systems commenced that

they are highly variable through both time and space, and this theme continues to permeate recent work (Frati *et al.* 2001; Sinclair 2001; Hugo *et al.* 2004; Lawley *et al.* 2004). However, how and why this variation changes with spatial and temporal scales across the range of ecosystems and species found in the terrestrial Antarctic has perhaps been less well appreciated. This is partly due to the fact that wide recognition of the significance of scale is relatively recent, and partly because data collection (both in the past and in the present) has tended to focus on certain areas, species and scales. For example, while Antarctic terrestrial biodiversity and the biogeography thereof is thought to be well known, many ice-free areas have yet to be systematically explored and investigations of several areas are surprisingly recent (Broady & Weinstein 1998; Convey *et al.* 2000a,b; Marshall & Chown 2002; Stevens & Hogg 2002; Bargagli *et al.* 2004; Convey & McInnes 2005; Peat *et al.* 2007). Moreover, no comprehensive database of the distributions of Antarctic and sub-Antarctic species yet exists (see Griffiths *et al.* 2003 for a marine example), although several non-digital compilations are now becoming available (e.g. Pugh 1993; Bednarek-Ochyra *et al.* 2000; Øvstedal & Lewis Smith 2001; Pugh & Scott 2002; Pugh *et al.* 2002; Ochyra *et al.* in press). Likewise, quantitative ecological work was, until relatively recently, restricted largely to several maritime and sub-Antarctic Islands (see Block 1984; Lewis Smith 1984; Hänel & Chown 1999 for access to this literature), although early work had commenced, but has not been systematically continued, elsewhere (Janetschek 1967). In a similar vein, although more than 27 springtail and 60 mite species have been recorded from the Antarctic continent, comprehensive investigations of the autecology, life histories and environmental responses of these groups have, until recently, been restricted to just a few species, most notably the springtail *Cryptopygus antarcticus* and the mite *Alaskozetes antarcticus* (Block 1984; Block & Convey 1995; Convey 1996a).

Over the past several years, however, this useful early work has been integrated into a broader picture of variation across a variety of spatial and temporal scales in both the genealogical and ecological hierarchies (Eldredge 1986). Indeed, it is now clear that Antarctic terrestrial biodiversity, while certainly poor from a global perspective, is characterized by substantial variability across a range of spatial and temporal scales, and that, as is the case elsewhere, the significance of the mechanisms underlying this variability varies from scale to scale. Here, we review what is presently known of spatial and temporal variability in Antarctic and terrestrial biodiversity and the mechanisms underlying this variation. In doing so, we discuss the implications of these findings for understanding the evolution of this diversity, and for its conservation at a time when Antarctica and its surrounding islands are experiencing considerable regional variation in their responses to global environmental change and the extent of human interest therein.

## 2. VARIATION ACROSS SPACE

Antarctic ice-free areas and the surrounding sub-Antarctic islands are isolated pockets of land in an area dominated by ice and ocean. Presently, of the Antarctic

continent's 14 million km<sup>2</sup>, only approximately 0.32% is ice-free (British Antarctic survey 2004) and available for use by terrestrial organisms, although even these areas are not fully used owing to extremes of the local environments (Janetschek 1970; Kennedy 1993; Convey & Lewis Smith 1997; Frati *et al.* 2001; Sinclair & Sjurson 2001). Moreover, the geological and glaciological histories of these ice-free areas differ substantially, which is not surprising given the size of the continent. Thus, both local and regional environmental variation determines the spatial variation of current diversity across the continent (Peck *et al.* 2006). Similarly, between 30 and 60° S the ratio of land to water is 1 : 1, whereas across the same latitudes in the Northern Hemisphere, the ratio is 16 : 1 (Chown *et al.* 2004). The influence of the Southern Ocean on the sub-Antarctic islands and the Antarctic continent, by way of climate and isolation, is therefore considerable. The islands also differ markedly in their glaciological and geological histories, including the extent of current glaciation (LeMasurier & Thomson 1990; Hall 2002). Again, this multi-scale spatial variation in the environment has profoundly affected the distribution of diversity on the islands (Chown *et al.* 1998, 2002; Greve *et al.* 2005).

#### (a) Individual and population levels

Spatial variation in individuals is more typical of plants and fungi than that of animals given that the latter do not tend to form spatially extensive patches, at least not in terrestrial systems. Nonetheless, a form of individual spatial variation is found in migratory birds and mammals that have significantly different diets and physiologies in their breeding and wintering grounds and during the transitions between them (though such variation is temporal too; Bearhop *et al.* 2003; Landys-Ciannelli *et al.* 2003). In the Antarctic, several migratory species, including seabirds, whales and seals move in and out of the region on a seasonal basis. These are all typically pelagic species, with the greater sheathbill (*Chionis alba*) representing the only terrestrial one. Little is known about the change in ecology of individuals during movements of this species.

In plants, the most extensive spatial work has concerned individual- and population-level genetic variations of mosses, typically from Victoria Land and mostly using random-amplified polymorphic DNA (RAPD; reviewed by Skotnicki *et al.* 2000), which is not without methodological problems (Rogers 2007). In several species, substantial variation occurs within clumps, such that although paired shoots are typically (though not always) identical, the distance between shoots increases with the decrease in relatedness (Selkirk *et al.* 1998; Skotnicki *et al.* 1998a,b, 1999a,b, 2002, 2004; Dale *et al.* 1999). This within-clump variation has been attributed to high rates of somatic mutation. Most mosses on the continent reproduce vegetatively—sporophyte maturation is rare, but not absent, and increases northwards along the Peninsula and to the sub-Antarctic (Convey & Lewis Smith 1993; Convey 1994; Lewis Smith & Convey 2002). Skotnicki *et al.* (2002) have noted that shoot tips growing even a few millimetres apart within a clump are separated by many years of growth and considerable UV-B exposure, which seems a probable cause of elevated levels of somatic

mutation characteristic of all of the mosses examined to date, given the known effects of UV-B radiation on mutagenesis (Ries *et al.* 2000, but see also Robinson *et al.* 2003). As a consequence of this somatic mutagenesis, genetic variability in Antarctic mosses is equal to or higher than that of sexually reproducing species found elsewhere (Skotnicki *et al.* 2000, 2004). Antarctic mosses may therefore provide an excellent model system for examining the importance of UV-B-associated somatic mutation for diversity in plants, although additional work is required to verify the extent of and reasons for this mutational change (Rogers 2007).

The significance of exploiting this model system might not seem obvious given that enhanced ultraviolet radiation typically has small physiological effects on Antarctic plants, and the plants also appear to be capable of rapid responses to changes in UV radiation (Huiskes *et al.* 2000; Newsham *et al.* 2002; Karentz 2003; Lud *et al.* 2003; Robinson *et al.* 2003). However, it has been suggested that ultraviolet-induced mutations and variation in the extent of UV radiation globally might be a cause of variation in speciation rates (Evans & Gaston 2005): one explanation for the global variation in species richness (the evolutionary-rates hypothesis; Rohde 1992; Willig *et al.* 2003). That both animals (Orme *et al.* 2005) and plants (Linder 2003) often show high local diversities in areas that have both high-incident UV and high water availability, but are not necessarily tropical (e.g. southwestern South Africa and Australia; high elevation areas in South America and Asia), perhaps deserves further exploration, especially given the evidence for UV effects on mutation rates in work on Antarctic species.

Genetic differences among moss populations have typically formed a major component of the RAPD analyses which have been undertaken. Variation among clumps varies significantly with quality of habitat; those areas with greater water supply typically have greater genetic variability (Skotnicki *et al.* 2000), though methodological issues might confound these conclusions. Patterns of variation also suggest substantially different colonization histories, with some sites showing evidence of multiple colonization events and little subsequent spread, and others indicating a single colonization and either substantial subsequent spread or pronounced antiquity of the population (Selkirk *et al.* 1997). The population-level analyses have also led these authors to suggest that long-distance dispersal is not uncommon, though the very fact that long-distance migrants can be detected suggests that the events might be rare (Rogers 2007). Wind is reputedly the primary agent responsible for dispersal over significant distances (Skotnicki *et al.* 1998b, 2001), while overland water flow during periods of elevated temperatures, when melt water is available, is responsible for local dispersal (Skotnicki *et al.* 2000).

Substantial differentiation of populations even at fine spatial scales has also been found in the few studies that have examined springtail genetic diversity. Allozyme investigations have revealed significant differentiation of *Gressittacantha terranova* associated with major glacial barriers in Victoria Land (Fanciulli *et al.* 2001; figure 1). In both this species and *Isotoma klovstadi* (assessed using the mitochondrial cytochrome *c* oxidase subunit II gene),



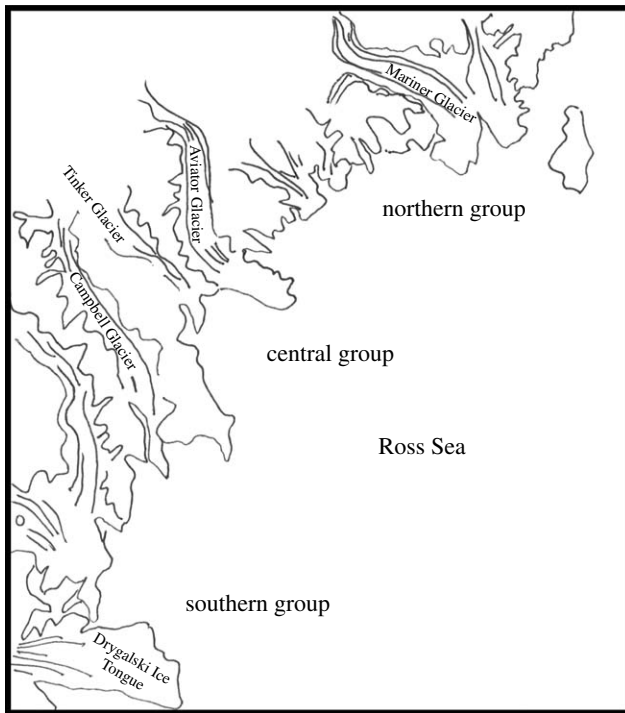


Figure 1. Division of populations of *G. terranovae* into northern, central and southern populations in Victoria Land on the basis of allozyme data. Adapted with permission from Fanciulli *et al.* (2001).

differences among populations are substantial. Although gene flow might have been higher in the past in *I. klovstadi*, it is now much reduced and dispersal rates in the population are very low (Frati *et al.* 2001). In *Gomphiocephalus hodgsoni*, another springtail species from Victoria Land, genetic isolation by distance is substantial, and extensive Pleistocene glaciations and limited dispersal capability have promoted isolation and divergence among its fragmented populations, which must once have been more widespread (though one recent dispersal event, by birds or humans, has taken place; Stevens & Hogg 2003). Low dispersal of springtails across what are essentially water-free landscapes (either ice or the dry terrestrial environments of the Dry Valleys and elsewhere) is not surprising given their limited desiccation resistance and tolerance (Harrisson *et al.* 1991; Hopkin 1997). However, dispersal by water is more probable (Coulson *et al.* 2002), but has not been investigated in Antarctic springtails other than on a very local scale (Hayward *et al.* 2004). The low tolerance of desiccation by springtails sets them apart from many other Antarctic organisms for which wind is a significant agent of dispersal (Marshall 1996, 1997; Marshall & Chalmers 1997; Marshall & Convey 1997; Muñoz *et al.* 2004).

Population genetic structure of indigenous sub-Antarctic springtail species is quite different from that of the Antarctic endemics. On Marion Island, indigenous species tend to show little isolation by distance, but rather structure indicative of recent expansion from glacial refugia (Myburgh *et al.* 2007). These species also show evidence of a more ancient pattern of population differentiation which in *C. a. travei* suggests that it colonized the islands shortly after they became subaerial some 500 000 years ago (McDougall *et al.* 2001).

The same rapid colonization of the Prince Edward Islands (of which Marion is one) seems to have taken place in at least one of the species of indigenous ectemnorhine weevils (Grobler *et al.* 2006), although the absence of a comparison with this species' closest putative ancestor means that the date of colonization must remain speculative. By contrast, in more recent invasive species, haplotype diversity is minimal, indicating a single colonization event. Analysis of the *COI* gene of many individuals of *Isotomurus cf. palustris* and *Ceratophysella denticulata* from across the island revealed that each species was represented by a single haplotype (Myburgh *et al.* 2007). Similarly, in the carabid beetle *Trechisibus antarcticus*, a relatively recent invader of South Georgia, apparently from the Falkland Islands, rare alleles are absent in the former population (Ernsting *et al.* 1995).

Variation among Antarctic populations is not restricted to the genetic level, as might be expected from knowledge of widespread species elsewhere (Spicer & Gaston 1999). Reproductive characteristics show substantial variation, with the extent of successful sexual reproduction in bryophytes declining with increasing latitude, though the signal can be spatially complex owing to variation in microclimates (Convey & Lewis Smith 1993; Convey 1996a; Lewis Smith & Convey 2002). The proportion of species (as distinct from individuals) occasionally recorded with sporophytes actually increases at higher latitudes (Lewis Smith & Convey 2002). Investment in reproduction in the mite *A. antarcticus* is also greater in northern (sub-Antarctic) than in southern (maritime Antarctic) populations, but little variation is found among the latter (Convey 1998). Physiological inertia has also been documented in the host-specific lepidopteran *Embryonopsis halticella* in the sub-Antarctic. Larvae on Marion Island and on Heard Island (separated by more than 1000 km) have statistically indistinguishable freezing points ( $-17$  to  $-20^{\circ}\text{C}$ ), upper lethal temperatures (approx.  $38^{\circ}\text{C}$ ) and survival times of dry conditions (Klok & Chown 2005). It is thought that larval physiological tolerances may have evolved as a response to cold dry conditions on the older Heard Island and have subsequently been retained in populations that colonized the younger Marion Island, which has a milder climate. However, not all groups show such inertia. For example, significant variation in critical thermal minima is found among populations of the freeze intolerant weevil *Palirhoeus eatoni* inhabiting Heard and Marion Islands, with populations on the former having lower values (Klok & Chown 2003).

Complex, among-population, altitudinal differences in body size of invertebrates have also been recorded in the region. On Marion Island, body size increases with altitude in all of the eurytopic weevil species (figure 2a), while on Heard Island the opposite pattern has been found (figure 2b; Chown & Klok 2003). Opposing latitudinal and altitudinal size clines have frequently been recorded in insects (Chown & Gaston 1999; Blanckenhorn & Demont 2004; Kozłowski *et al.* 2004), and can be explained in an adaptive context of body size optimization given seasonal constraints on growth and development and life cycle duration (Roff 1980; Kozłowski *et al.* 2004). Differences in seasonality of

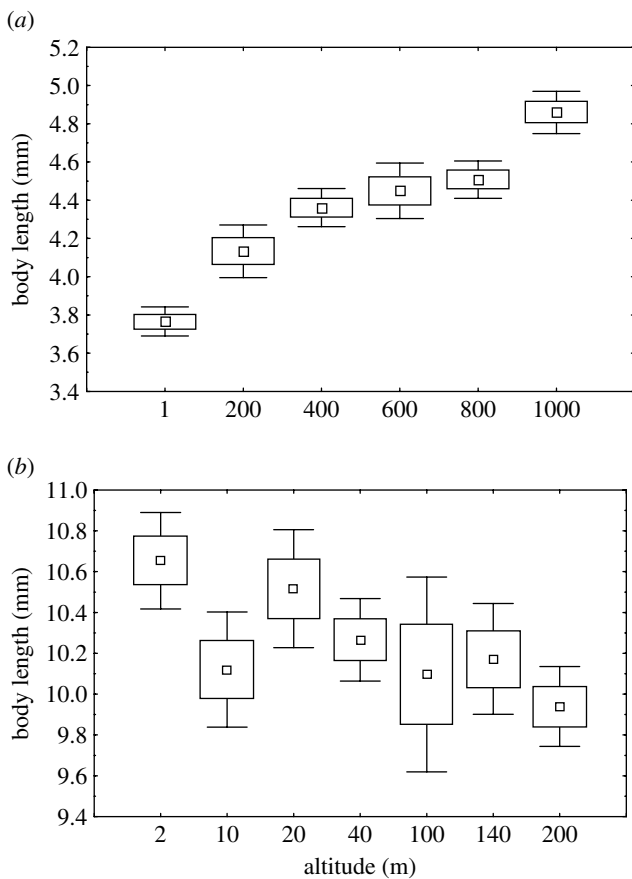


Figure 2. Body length variation across an altitudinal gradient in (a) *Bothrometopus parvulus* at Marion Island and (b) *Ectemnorhinus viridis* at Heard Island. Data are presented as mean, s.e. and 95% CI. Adapted with permission from Chown & Klok (2003).

Heard and Marion Islands, which lie below and above the Antarctic Polar Frontal Zone, respectively, are thought to be a major reason for the differences in size clines (Chown & Klok 2003).

### (b) Species level

How long particular species have occurred in Antarctica, or on the sub-Antarctic islands, and what determines species incidences and abundances, are questions that have long occupied ecologists and systematists working in the region (Skottsberg 1960; Gressitt 1965, 1971; Janetschek 1967, 1970; Lewis Smith 1984). Very low species endemism in some groups, particularly the mosses (Bednarek-Ochyra *et al.* 2000; Peat *et al.* 2007; Ochyra *et al.* in press), combined with substantially more extensive glaciation of the Antarctic during the last glacial maximum than at present (Peck *et al.* 2006), has encouraged the view that the majority of Antarctic species are relatively recent arrivals, with perhaps a few microbial or protozoan taxa being substantially older. However, recent work has altered this perspective. It now seems that mosses may have an atypical pattern of endemism compared with most other major groups of Antarctic flora and fauna, and that the generalization of an assumption of recent origin may be little more than dogma. In the continental Antarctic, it is clear that several areas (e.g. parts of the Victoria Land Dry Valleys, Transantarctic Mountains, some inland

nunatak groups) have remained ice-free since at least the end of the Miocene (Boyer 1979; Prentice *et al.* 1993). Careful reassessment of some continental Antarctic mite distributions has indicated that the majority of species are probably pre-Pleistocene endemics, and that speciation in some groups, such as the endemic oribatid genus *Maudheimia*, is in keeping with models of the development of the East Antarctic ice sheet (Marshall & Pugh 1996; Marshall & Coetzee 2000). The West Antarctic remains problematic, because the large majority of biota are present in coastal and low-altitude locations, which glacial and ice sheet reconstructions indicate would have been obliterated at glacial maximum by ice sheets extending out to the point of continental shelf drop-off. Thus, the existence and location of potential refuge regions remain hypothetical (Convey 2003a). Nevertheless, evidence is increasing for the presence of an ancient and vicariant biota, such as species of endemic midges (Diptera: Chironomidae) whose age of evolutionary separation has been estimated using a 'molecular clock' approach at 20–40 Myr, in keeping with the opening of the Drake Passage (Allegrucci *et al.* 2006). It is also clear that many Antarctic nematodes are endemic to either the continental or maritime Antarctic, strongly suggesting that they are glacial survivors rather than post-glacial colonists (Andrássy 1998; Maslen & Convey 2006). Recent work on springtails has demonstrated ancient (11–21 Myr) divergence associated with glaciation of Antarctica, but much younger colonization events among sub-Antarctic islands (less than 2 Myr; Stevens *et al.* 2006).

For small organisms, such as microbes and ciliates, it has been suggested that global diversity is low because substantial global dispersal of the propagules of these species hampers isolation and consequently speciation (Fenchel 1993; Finlay *et al.* 1996; Wilkinson 2001; Finlay 2002). In other words, most species in these groups should be virtually cosmopolitan, and should include the Antarctic within their ranges, with their distribution limited by their ecophysiological abilities to survive the challenges of the Antarctic environment, rather than by the process of dispersal *per se*. However, modern investigations of both prokaryote and eukaryote diversities in Antarctica provide little support for the idea, given low relatedness of Antarctic taxa to those in existing sequence databases (Franzmann 1996; Lawley *et al.* 2004). Although Vincent (2000) cautioned that lack of sequence data from elsewhere and insufficient taxonomic resolution might compromise conclusions of substantial endemism in Antarctica, other taxa show similar levels of endemism (see above). Work in temperate regions is also starting to show that the ecological biogeography of microbes and other small organisms is similar to that of the macrobiota (Green *et al.* 2004; Horner-Devine *et al.* 2004; Smith *et al.* 2005).

Endemism can also be high across the sub-Antarctic, although this differs among taxa. In vagile taxa, such as the bryophytes and lichens, endemism tends to be low (acknowledging that further survey and taxonomic work might change the situation; Øvstedal & Gremmen 2001; Muñoz *et al.* 2004), while in insects, it is more variable. In islands close to continental or other

Table 1. Variance partitioning (Legendre & Legendre 1998) from generalized linear models of the effects of environmental and spatial variables on the abundance of springtails at Cape Hallett, Northern Victoria Land. Values are percentage deviance explained (Sinclair *et al.* 2006).

model	space	spatially structured environmental	environmental	unexplained
soil				
<i>Cryptopygus cisantarcticus</i>	56.3	4.1	19.6	20.0
<i>Isotoma klovstadi</i>	39.4	27.3	16.5	16.8
stones				
<i>Cryptopygus cisantarcticus</i>	8.4	19.2	33.9	38.5
<i>Friesea grisea</i>	16.4	17.8	51.1	14.7
<i>Isotoma klovstadi</i>	39.0	14.5	0.5	54.0
<i>Stereotydeus belli</i>	0.0	0.0	40.1	59.9
<i>Tydeus setsukoae</i>	11.8	15.7	16.3	56.2

landmasses genera and sometimes species are shared with what appears to be the source areas (Kuschel 1971; Vogel 1985; Marris 2000), while in more distant archipelagos, endemism is high and relationships are enigmatic. Indeed, the origin and closest relatives of many of the insect taxa from the South Indian Ocean Province Islands (Prince Edward Islands, Crozet Islands, Kerguelen Islands, Heard and McDonald Islands) remain a subject of vigorous contention, as they have been since the discovery of these species (see Jeannel 1964 for early discussion and Greve *et al.* 2005 for recent partial review).

Although regional species pools and biogeographic history might determine what species can potentially occur at a given site, actual occurrence is determined by site suitability. Investigations of site suitability at the species level (e.g. incidence functions across a range of habitable patches; Ovaskainen & Hanski 2003) are not typical of the Antarctic literature (but see Usher & Booth 1984, 1986). Nonetheless, the determinants of local scale occupancy and abundance have been extensively investigated across a range of sites. Water availability, temperature (which also influences water availability), protection from wind, the availability of nutrients (often nitrogen and also carbon—many continental Antarctic systems are poor in carbon), the extent of lateral water movement, and the extent of soil movement and ice formation all have a pronounced effect on the suitability of sites for colonization, growth and reproduction (Janetschek 1970; Lewis Smith 1984; Ryan & Watkins 1989; Kennedy 1993; Convey 1996a; Freckman & Virginia 1997; Convey *et al.* 2000a; Sinclair 2001; Smith *et al.* 2001). Of these, water availability (and the elevated temperatures that drive it) is thought to be most significant on the Antarctic continent and peninsula, while nutrient availability, soil water movement and temperature are most significant in the sub-Antarctic. Most authors have concluded that, at least on the continent, extreme abiotic conditions preclude life in many ice-free areas and that, unlike the situation across most of the planet, abiotic rather than biotic stressors exert a controlling influence on life histories (Janetschek 1970; Convey 1996a; Wall & Virginia 1999).

If spatially aggregated, suitable abiotic conditions are major drivers of the incidence and abundance of many Antarctic organisms, it might be expected that a

few key environmental and spatial terms would explain a large proportion of the variance in incidence or abundance (depending on the scale of the study; Usher & Booth 1986). Such an approach has rarely been applied to modelling the abundance and distribution of Antarctic species (most investigations focus on the assemblage level). Where this has been done, spatial structure has typically not been considered despite wide acceptance of its importance in ecology (Legendre 1993; Thomson *et al.* 1996; Liebhold & Gurevitch 2002). Notable exceptions are the studies by Usher & Booth (1984, 1986), which appear to have been limited only by the availability of appropriate analytical techniques. Other Antarctic studies have either examined the relationship between abundances and environmental variables directly (Freckman & Virginia 1997; Courtright *et al.* 2001; Sinclair & Sjørnsen 2001), or have sought to assess the habitat specificity and fidelity of species without explicit reference to underlying environmental variables (Mercer *et al.* 2000; Barendse *et al.* 2002). However, in a recent investigation of the abundance structure of several arthropod species at Cape Hallett (Northern Victoria Land; Sinclair *et al.* 2006), spatially explicit analytical methods were used. Although temperature and chlorophyll-a availability were not included as variables in the models (despite their importance in determining arthropod abundance; Sinclair & Sjørnsen 2001), the models including spatial and environmental terms explained between 60 and 86% of the variation in abundance of each of three springtail species (table 1), which is high by comparison with invertebrates elsewhere (Brewer & Gaston 2002; McGeoch & Price 2004). Soil properties (excluding assessments of spatial pattern) explain 40–50% of spatial abundance variation in nematodes in Taylor Valley (Powers *et al.* 1998). Therefore, it appears that spatial and environmental variables do explain much of the variation in the abundance of individual species. However, explanatory power depends on both the scale of investigation and the taxa considered (Usher & Booth 1986). Further, explicit modelling work is required to determine whether the abundance structure of Antarctic arthropods can be more readily explained by a few environmental and spatial variables than is the case for species from more temperate environments.



Qualitative work on species incidences has mostly focused on determinants of habitat specificity. In the sub-Antarctic, it appears that species occupying the epilithic biotope (fellfield, coastal rockfaces) have greater habitat specificity and have occurred in these habitats for much longer, surviving glaciations in epilithic refugia, than species from the typically post-glacial vegetated biotope (Chown 1990a, 1994; Barendse *et al.* 2002). A global analysis of habitat specificity in ameronothroid mites has revealed a similar pattern in south and north polar species (Marshall & Convey 2004). Habitat specificity tends to decline towards the poles. In the Antarctic region, species such as *A. antarcticus* and *Halozetes belgicae* occupy a range of terrestrial habitats at high latitudes, but are almost exclusively supralittoral in the sub-Antarctic. The most plausible explanation for these patterns is recent post-glacial colonization of the ice-free areas (Marshall & Convey 2004). Phylogeographic analysis (Avisé *et al.* 1987) across a range of sites could be used to test these ideas, but to date such work is rare in the Antarctic region (§2a).

### (c) *Assemblage and ecosystem levels*

Unlike Antarctic marine systems (Clarke & Johnston 2003), and terrestrial environments elsewhere, the terrestrial ecosystems of the continental and maritime Antarctic are species poor (Convey 2001). Some sites are characterized by less than a dozen invertebrate and plant species, in others, life is restricted to depauperate endolithic communities in sandstone rocks or gypsum crusts, and at the limit many ice-free areas seem totally devoid of life (Broady & Weinstein 1998; Wall & Virginia 1999; Hughes & Lawley 2003; Cockell & Stokes 2004; Convey & McInnes 2005). Nonetheless, substantial spatial complexity in the richness and identity of species is found across Antarctica. At a large scale, species richness increases with a decline in latitude (Block 1984; Broady 1996; Smith 1996), but the pattern is spatially complex rather than monotonic (Clarke 2003). For example, in the maritime Antarctic, soil eukaryote microbial diversity is as high at approximately 71–72° S as it is at approximately 60–67° S, and only declines steeply beyond 74° S (Lawley *et al.* 2004). Likewise, in West Antarctic Alexander Island and East Antarctic Dronning Maud Land, the metazoan microfauna shows evidence of a complex pattern of richness across ice-free areas (Sohlenius *et al.* 1996; Sohlenius & Boström 2005; Maslen & Convey 2006). Similar patterns of complexity are emerging for mosses and lichens (Clarke 2003; Peat *et al.* 2007), as taxonomic resolution and sampling coverage improves. Complex spatial variation in richness is not unexpected, given that it is characteristic of life elsewhere on the planet (Gaston 2000). However, owing to relatively poor sampling across the ice-free areas of the Antarctic continent, it is not possible to discern whether any systematic trends characterize this large-scale richness variation. Therefore, the identification of any underlying mechanisms (beyond local scale factors influencing site suitability, see §2b above) is still some way off.

Early biogeographic work divided the Antarctic region into continental and maritime Antarctic, and sub-Antarctic (reviewed in Lewis Smith 1984). Recent work

has identified a much clearer distinction between the Antarctic Peninsula and the remainder of continental Antarctica than previously recognized. Indeed, there is a particularly striking lack of overlap at species level between the representatives of several higher-order taxonomic groups. Thus, the most recent taxonomic treatments indicate that there is no overlap at species level between these regions for nematodes (Andrássy 1998) and free-living mites (Pugh 1993), and that only a single springtail species is shared (Greenslade 1995). Other groups, such as tardigrades, show an intermediate level of species overlap (approx. 50%; Convey & McInnes 2005), while bryophytes, as mentioned earlier, appear to show a completely different pattern of biodiversity, with very few (less than five species) or possibly even no endemism across the entire continent. Although the Antarctic terrestrial biota are individually less spectacular, the strength of this separation between the two regions is reminiscent of the much better known 'Wallace Line' of Southeast Asia (Brown & Lomolino 1998), and is likewise indicative of ancient and different evolutionary origins of their biota. Such is its biogeographic significance that we propose the adoption of a similarly named feature, the Gressitt Line, to emphasize the boundary between these two regions. It is named in recognition of the fundamental contribution of J. L. Gressitt to the early development of understanding of Antarctic and Southern Ocean terrestrial biogeography during the 1960s and 1970s (figure 3). Although, as with much of Antarctica, there remain many specific unsurveyed locations in the region of this boundary, it lies (i) south of Alexander Island and the English and Bryan Coasts, whose biota includes maritime rather than continental affinities (Peat *et al.* 2007), (ii) north of the inland Ellsworth Land nunatak ranges (Sky Hi and Sweeney Nunataks, Hauberg Mountains), whose fauna has continental affinities (Convey & McInnes 2005), and (iii) on the east coast of the Antarctic Peninsula south of the Wakefield Mountains, whose very limited known mite fauna is maritime in origin (P. Convey & P. J. A. Pugh 2005, unpublished data).

By comparison with the continental and maritime Antarctic, the Southern Ocean islands are species rich and well surveyed, at least for taxa such as insects and vascular plants (Vernon & Voisin 1990; Dreux & Voisin 1993; Chown *et al.* 1998, 2006; Gremmen & Smith 1999; Frenot *et al.* 2001; Jones *et al.* 2003). Moreover, patterns in species richness and the mechanisms underlying these patterns have been comprehensively investigated (Chown *et al.* 1998, 2001, 2005; Greve *et al.* 2005). Across the islands, species richness of indigenous and alien vascular plants covaries significantly with available energy and the same is true of indigenous and alien insect species richness. The richness of alien insects and vascular plants also covaries with human visitor frequency to the islands. Positive relationships between energy availability and species richness have been documented in many systems and at a wide variety of spatial scales (Waide *et al.* 1999; Hawkins *et al.* 2003), and are considered one of only a few ecological laws (Rosenzweig 1995). However, the mechanisms underlying positive species–energy relationships remain contentious (Evans & Gaston 2005; Evans *et al.* 2005), as do explanations

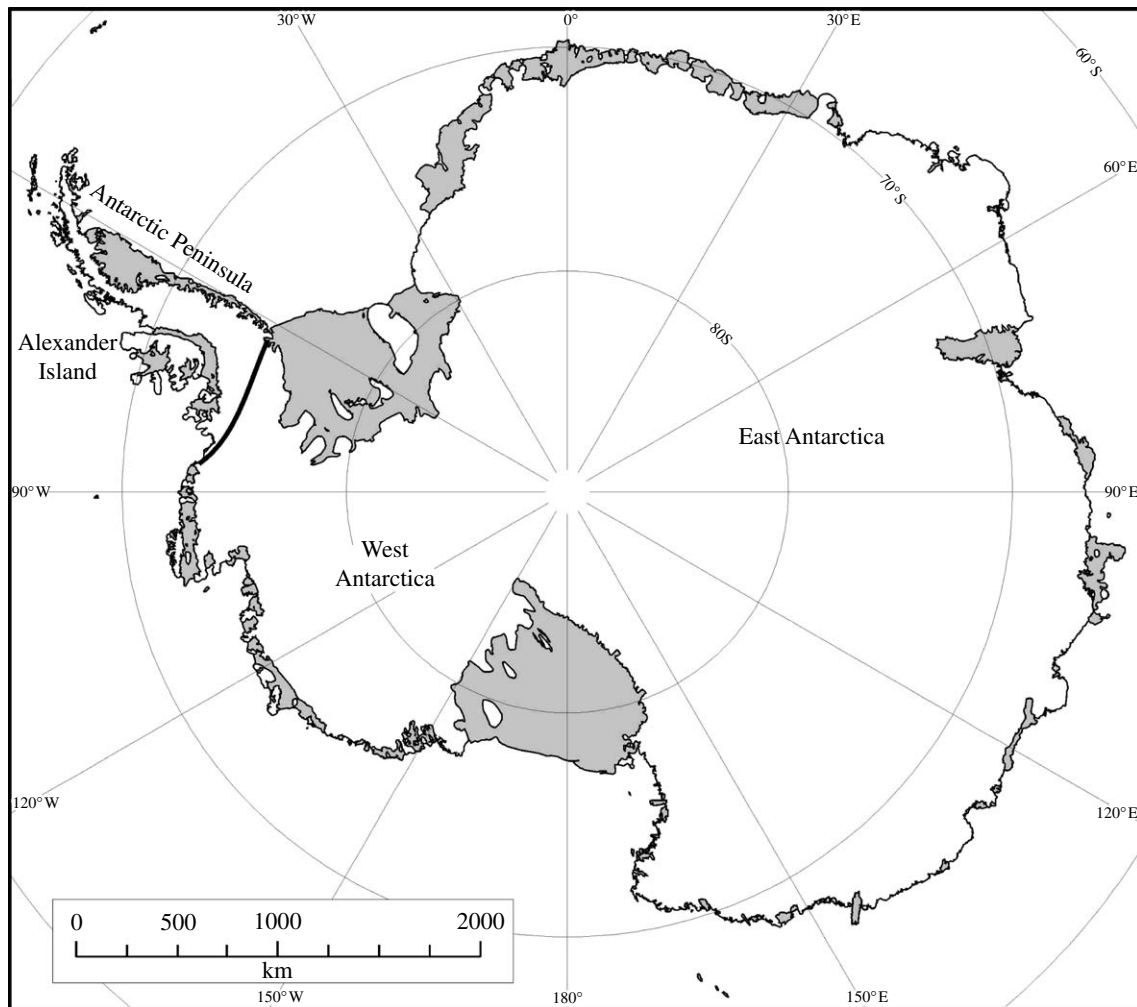


Figure 3. Map of the 'Gressitt Line', a strong biogeographic region of separation between the biota of the Antarctic Peninsula and continental Antarctica.

for spatial variation in species richness generally (Willig *et al.* 2003), despite the antiquity of the pattern. Current data for the Southern Ocean islands preclude identification of a mechanism underlying these positive species–energy relationships. Nonetheless, that strong positive relationships exist for both alien and indigenous species on islands which are characterized by relatively high levels of endemism provides some insight into probable mechanisms.

The species richness of an area is determined by four processes: speciation; extinction; immigration; and emigration. For isolated islands such as those of the Southern Ocean, and in indigenous taxa such as vascular plants and insects, immigration has probably been low owing to the considerable distance of the islands from source areas (Chown *et al.* 1998, but see also Greenslade *et al.* 1999). Moreover, high endemism (Chown 1990a; Greve *et al.* 2005) indicates substantial *in situ* speciation. Little data exist for emigration and extinction (but see Convey *et al.* (2000b) for examples of proposed short-term colonization and then extinction associated with ephemeral geothermally active locations on the maritime Antarctic South Sandwich Islands). Indigenous species are often found in the aerial plankton (Marshall & Convey 1997; Peck *et al.* 2006) and palynological analyses of interglacial peat lenses and lake sediments indicate the presence of taxa that are now absent (Scott & Hall 1983; Barnes *et al.* 2006). Thus, for

indigenous taxa, mechanisms that both generate species and cause their removal, and which are related to energy variation, are likely to be responsible for the positive relationship between richness and energy availability. These mechanisms include enhanced evolutionary rates (Rohde 1992; Evans & Gaston 2005) and reduced extinction rates as a consequence of increased population size (Chown & Gaston 2000; Evans *et al.* 2005) under conditions of higher energy availability. However, it is difficult to envisage any mechanism associated with elevated speciation rates causing the relationship between alien species richness and energy availability. After all, the alien species have immigrated to the islands as a consequence of direct or indirect human intervention (Chown *et al.* 1998; Frenot *et al.* 2005). Thus, only two mechanisms and their interaction can explain a positive alien species–energy relationship: the ecological processes that enable large numbers of species to coexist (Gaston 2000; Evans *et al.* 2005), and the historical processes that have meant enhanced propagule pressure as a consequence of high visitor frequency (Lonsdale 1999; McKinney 2002). Both sets of processes are largely to do with the ways in which increases in abundance reduce the chances of extinction typically associated with small populations. Therefore, it would seem that, at least in alien species, positive species–energy relationships are established rapidly owing to spatial variation in extinction rates associated with



spatial variation in energy availability. Indeed, it is clear that the majority of the phases of invasion identified for plants (Richardson & van Wilgen 2004) typically are to do with avoidance of rarity and extinction. The sole exception is arrival, which is associated with transport success and the survival of individuals during the process.

Ultimately, variation in extinction rates cannot be the only process determining spatial variation in richness for all species: new species must arise at some point if richness is not to show a long-term temporal decline (which is what happens in neutral models with no speciation or immigration from the metacommunity; Hubbell 2001). However, the rapid development of alien richness–energy relationships (most introductions to the Southern Ocean islands have taken place over the past 200 years; Gaston *et al.* 2003; Chown *et al.* 2005) suggests that spatial variation in speciation rate need not be spatially concordant with variation in richness, but might show a more complex pattern. By contrast, spatial variation in extinction rate should follow richness more closely.

Richness is only one property of assemblages, others being the subdivision of individuals and biomass among each of the species found in the assemblages, the body size and range size of each of the species, and the trophic interactions among the species and their constituent individuals (Blackburn & Gaston 2001b; Bell 2003; Cohen *et al.* 2003, 2005). Composite assemblage properties and their underlying correlates have been examined for a wide range of Antarctic and sub-Antarctic ecosystems, typically using multivariate techniques, and spatial variation in the abundances of individual species has also been investigated across a range of sites (Goddard 1979; Block 1982; Smith & French 1988; Ryan & Watkins 1989; Courtright *et al.* 2001; Gabriel *et al.* 2001; Sinclair & Sjørnsen 2001). Assemblage properties that are the stuff of modern macroecological analyses have enjoyed less attention, despite the fact that these species-poor systems lend themselves to this kind of analysis. For example, Gaston *et al.* (2001) provided the most complete animal species–body size frequency distribution for any system globally by compiling and analysing these data for the well-surveyed Marion Island. Likewise, although early work was concerned with food webs in the Antarctic, largely as a consequence of the International Biosphere Programme (Block 1984, 1985), little subsequent work has taken place (though see Wall & Virginia 1999). Nonetheless, Antarctic systems are remarkable from a food web perspective because predation and parasitism are either low or non-existent, herbivory is uncommon, and biological invasions, which are being documented more frequently across the Antarctic (Frenot *et al.* 2005), have probably significantly altered food web structure, leading to trophic cascades (Crafford & Scholtz 1987; Bergstrom & Chown 1999).

### 3. VARIATION THROUGH TIME

Over geological time, biodiversity in Antarctica and on the sub-Antarctic islands has varied considerably. The continent was once home to a diverse flora (Quilty 1990) and a fauna that included dinosaurs (Hammer & Hickerson 1994), the earliest representatives of the globe's modern avifauna (Clarke *et al.* 2005), and

presumably a wide variety of insects (Ashworth & Kuschel 2003). Likewise, extensive fossil floras characterized the oldest of the sub-Antarctic islands on the Kerguelen Plateau (Chastain 1958; Quilty & Wheller 2000). Over shorter time-scales, palynological evidence has demonstrated compositional change in the floras of many sites (Scott 1985), and lake sediment cores have also revealed substantial variation in the abundances of terrestrial and freshwater invertebrates such as mites and crustaceans (Cromer *et al.* 2006; Hodgson & Convey 2006). Interest in temporal variation in Antarctic terrestrial systems was initially focused on seasonal changes in the abundances, phenology and life histories of plants and animals, and on successional changes in plant communities (reviewed in Block 1984; Lewis Smith 1984; Convey 1996a). More recently, the realized and probable impacts of global environmental change have come to dominate research interest (Smith & Steenkamp 1990; Lewis Smith 1994; Block & Harrison 1995; Kennedy 1995a; Bergstrom & Chown 1999; Walther *et al.* 2002; Convey 2003a; Robinson *et al.* 2003), especially owing to the rapid rates of climate change along parts of the Antarctic Peninsula and at the sub-Antarctic islands (King *et al.* 2003), increasing numbers of biological invasions (Frenot *et al.* 2005), and the rise in human traffic to the region (Naveen *et al.* 2001). Nonetheless, temporal variation in diversity has been documented across a broad range of scales in the Antarctic region.

#### (a) Individual level

Individuals vary across a range of temporal scales. Various physiological, life-history and morphological traits (all form part of biodiversity; Spicer & Gaston 1999; Roy *et al.* 2001) change with ontogeny, ageing, nutrient availability, diurnal cycle and season. Such change is often discussed under the rubric of phenotypic plasticity, and the literature on this topic is large (West-Eberhard 2003; De Witt & Scheiner 2004; Chown & Terblanche 2007). Much of it is concerned with the contentious question of what conditions should promote adaptive phenotypic plasticity (De Witt & Scheiner 2004; Chown & Terblanche 2007). To some extent, the controversy has been fuelled by the difficulty of establishing a direct link between trait variation and fitness (Feder 1987; Angilletta *et al.* 2002), and by the absence of critical hypothesis testing (Huey & Berrigan 1996). Moreover, it has not always been appreciated that phenotypic plasticity (or its absence) in a given trait must be seen in the context of the character complex of which the trait is a part, and the overall contribution of the trait to fitness (Woods & Harrison 2002; Pigliucci 2003).

Antarctic plants and animals are typically characterized as having 'very flexible' life histories (Convey 1996a), which are thought to enable them to survive a low temperature, dry (at least on the continent) and seasonally variable environment. Seasonal variation in a wide range of physiological traits has been investigated in several species of plants and animals (Sømme & Block 1982; Convey 1996a; Convey *et al.* 2003; Slabber & Chown 2005). However, recent work has also demonstrated that responses to

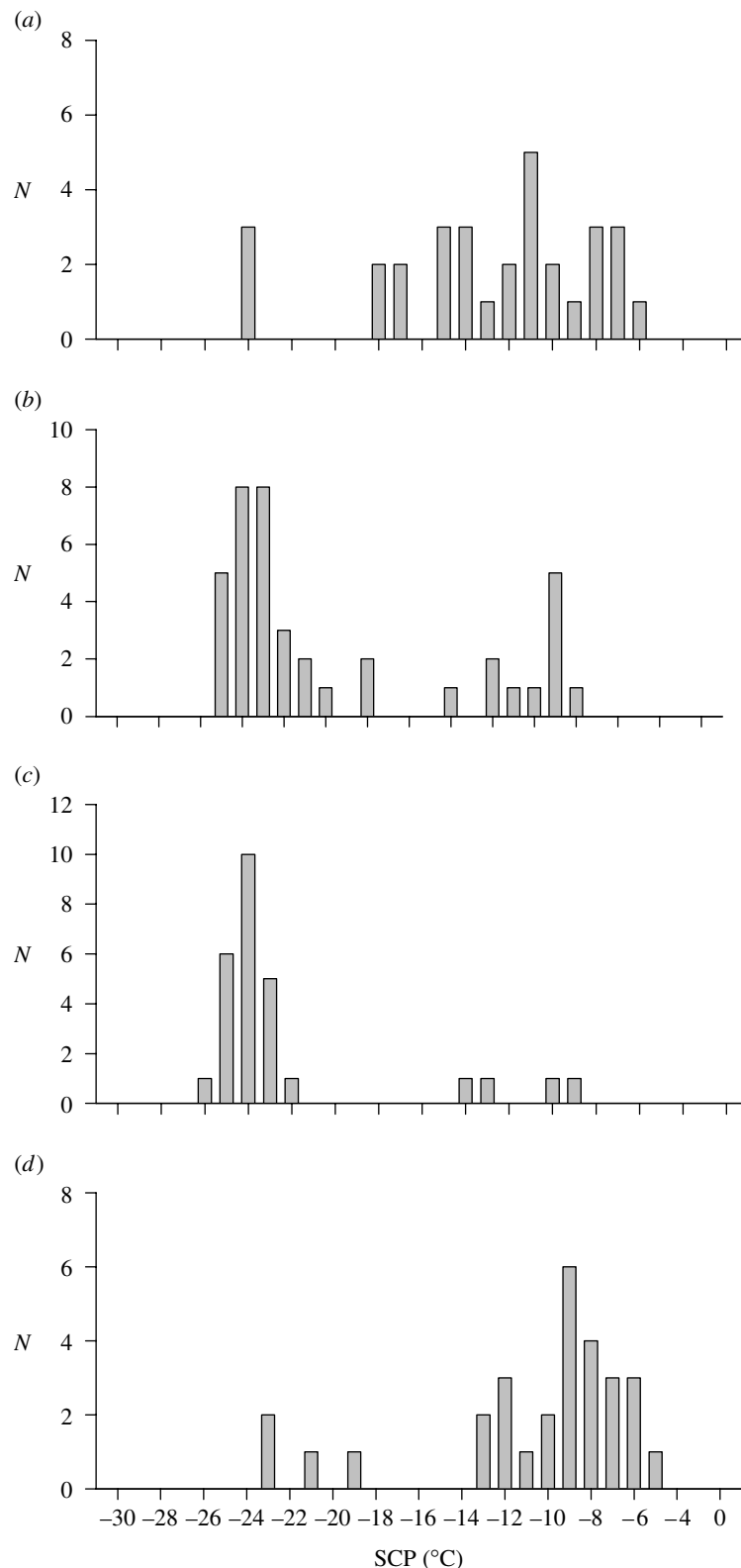


Figure 4. Supercooling point (SCP) distributions in the springtail *C. denticulata* from (a) an 'arbitrary' field sample, (b) pre-moulting animals from the same main sample, (c) recently moulted animals and (d) recently moulted animals that had been fed for 1 day (10°C). Note the decline in SCP with moulting. Adapted with permission from [Worland \*et al.\* \(2006\)](#).

environmental variation can be even more rapid. For example, supercooling point (or freezing point) can vary within a matter of hours in response to decreasing or increasing temperatures in the springtail *C. antarcticus* and in the mites *A. antarcticus* and *H. belgicae*, although the mechanisms underlying such rapid responses have yet to be fully elucidated ([Worland & Convey 2001](#)). Similar responses have since been found

in the East Antarctic springtail species *Isotoma klovstadi* and *Cryptopygus cisantarcticus* (but not in *Friesea grisea*; [Sinclair \*et al.\* 2003a](#)). Short-term variation in the moulting status of a springtail also has a dramatic effect on its freezing point, as has been demonstrated in population-level analyses of the indigenous *Tullbergia antarctica* ([Worland 2005](#)) and the invasive species *Ceratophysella denticulata* on sub-Antarctic Marion

Island (figure 4; Worland *et al.* 2006). Moulting effects on supercooling points mean that previously adaptive interpretations of supercooling point variation might have to be reinterpreted. Rapid responses have also been reported in field studies of pigment biochemistry of species of moss and liverwort on maritime Antarctic Adelaide Island. Non-manipulated plants, exposed to naturally varying levels of ultraviolet B radiation associated with the dynamically changing depth of the Antarctic ozone hole, showed rapid changes in the concentrations of some screening pigments that were best correlated with the levels of UV-B experienced within the previous 24 h rather than any longer period (Newsham *et al.* 2002; Newsham 2003). It is recognized that any such rapid biochemical and ecophysiological responses carry clear implications in terms of the diversion or trade-off of energy resources, an important factor determining life-history strategies (Convey 1996a, 1998, 2003a), but to date little or no effort has been directed towards quantifying these shifts in energy budgets.

Antarctic terrestrial organisms are not only thought to be flexible in their strategies, but also appear to be especially capable of responding to unpredictable environmental variation (Convey 1996a). Unpredictability over short time-scales is thought to be a major feature of Antarctic terrestrial environments (Peck *et al.* 2006). Rapid responses in supercooling points of Antarctic springtails are clearly one form of response to this unpredictability. Another is the preponderance of freezing tolerance (i.e. the capability of surviving extracellular and perhaps partial intracellular ice-formation; Sinclair *et al.* 2003b) in sub-Antarctic insects (excluding springtails). The large majority of the species that have been investigated are not only able to survive freezing, but do so typically only to a few degrees below their freezing points, making them moderately freezing tolerant (Klok & Chown 1997; Van der Merwe *et al.* 1997). Subsequent work has demonstrated that this is true of Southern Hemisphere insects in general, by comparison with their freeze intolerant Northern Hemisphere counterparts (Sinclair *et al.* 2003c; Sinclair & Chown 2005a), though the complexities of phylogenetic inertia and key innovations in certain groups require further investigation. In much of the temperate to cold Southern Hemisphere, winter temperatures fluctuate around 0°C, the freezing point of water. Thus, insects have to be capable of responding to rapid and unpredictable freezing events. Freeze intolerance typically requires substantial preparation by individual insects, including gut clearance and the production of various anti-freeze compounds (Chown & Nicolson 2004). Substantial preparatory change is also typical of strong freezing tolerance (where death takes place tens of degree below the freezing point), though some Antarctic nematodes can do this with apparent ease under laboratory conditions (Convey & Worland 2000). By contrast, moderate freezing tolerance does not appear to require substantial preparatory change and ice nucleation from gut material would have no deleterious effects. Thus, insects can simply freeze during cold snaps (which are typically not severe) and then return to their normal feeding activities (though see also Sinclair & Chown 2005b). Selection to survive an environment that

fluctuates around 0°C either for most of winter or for much of the year appears to have favoured moderate freezing tolerance (Sinclair & Chown 2005a). Moreover, in many species from the sub-Antarctic islands, seasonal variation in cold hardiness strategy is not nearly as marked as it is elsewhere, in keeping with a strategy tuned to coping with an unpredictable environment.

Environmental unpredictability (i.e. creating the risk of inappropriate responses to misleading environmental cues) is also thought to be a primary reason why phenotypic plasticity in some traits might not be favoured (Chown & Terblanche 2007), and has been suggested as underlying the absence of 'true' diapause within the life cycles of Antarctic invertebrates (Convey 1996b). This certainly seems to be the case for several traits in mites and insects on sub-Antarctic Marion Island. By comparison with more temperate sites, temperatures at Marion Island are highly unpredictable from day-to-day (figure 5). This seems to be a major reason why acclimation responses in many traits are virtually non-existent, including locomotion traits and supercooling points in acarid mites (Deere & Chown 2006; Deere *et al.* 2006), supercooling points in a flightless moth (Sinclair & Chown 2003) and rapid cold hardening in a kelp fly (Terblanche *et al.* 2007). However, responses to acclimation are present in other traits, notably critical thermal minima in beetles, and this trait and supercooling points in another flightless moth species (Klok & Chown 1998, 2003), and several thermal tolerance traits in springtails (Slabber *et al.* 2007). Unfortunately, it is not yet known why traits vary in their response to acclimation, although some difference between indigenous and invasive species exists. However, studies elsewhere have demonstrated that even closely related tolerance traits can be controlled by different genes and respond quite differently to acclimation or selection (reviewed in Hoffmann *et al.* 2003; Chown & Nicolson 2004). Unravelling the relationships between environmental predictability, trait variation and fitness would be a useful avenue for future terrestrial research in the Antarctic (Peck *et al.* 2006).

#### (b) Population level

To some extent, population-level analyses have been used as a means to identify individual-level variation in traits such as the influence of moulting on supercooling points (Worland 2005; Worland *et al.* 2006), so blurring the distinction between the two. Nonetheless, substantial population-level work on temporal variation has been undertaken in its own right. Much of this work has focused on the reproductive phenology of both plants and animals and changes in the abundances and activities of invertebrate populations over one or more seasons (Lewis Smith 1984; Convey 1996a). The latter work has demonstrated that the extent to which abundance fluctuates with season, and the months in which peak abundances may occur, vary significantly between different species at different sites (Block 1982; West 1982; Barendse & Chown 2001). Moreover, the three-dimensional spatial distribution of individuals also changes substantively with season (Goddard 1979).

Over the longer term, it is clear that at least on the Antarctic Peninsula and on the sub-Antarctic Islands,



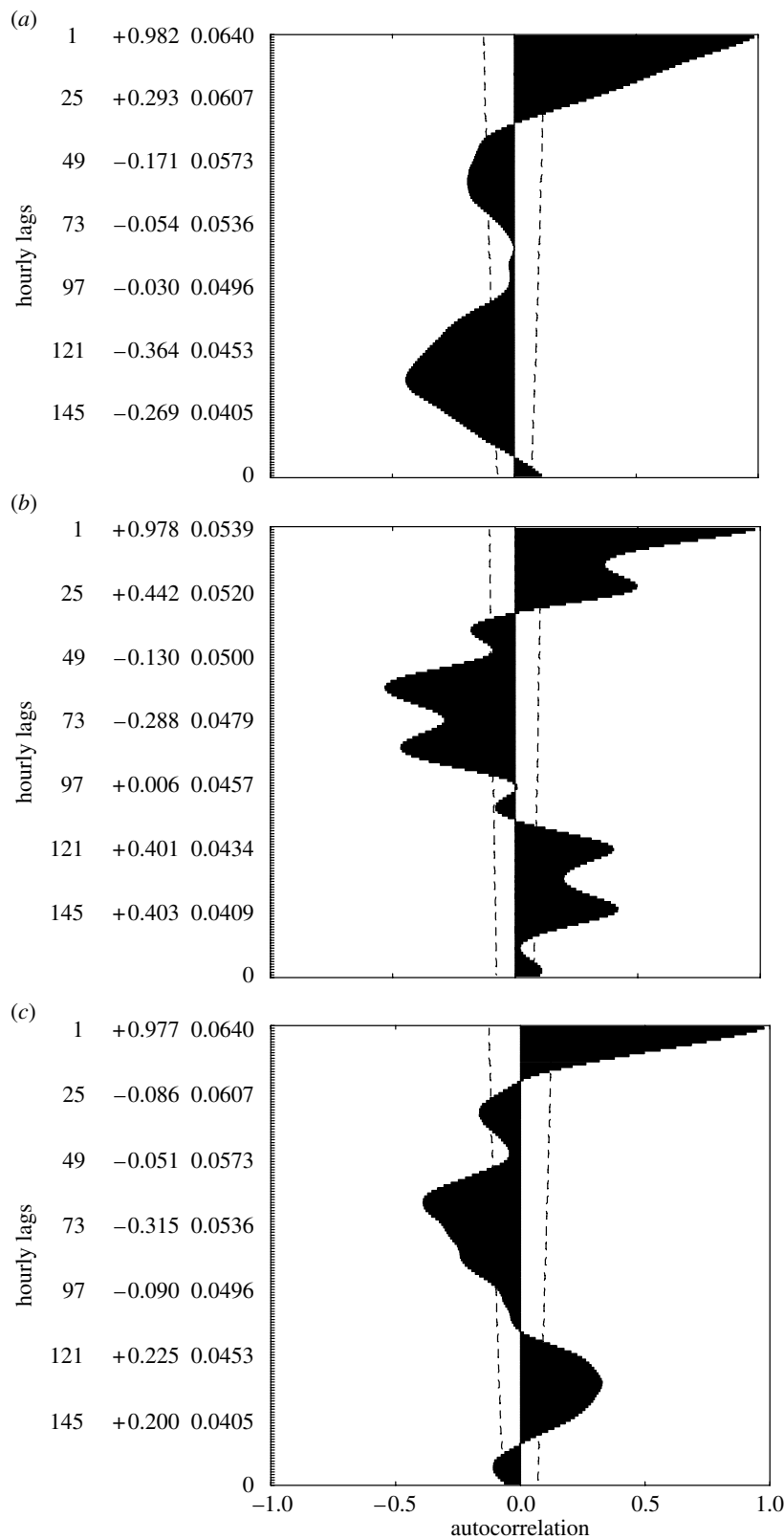


Figure 5. Autocorrelation plots for hourly microclimate temperatures recorded on Marion Island during (a) August 2002, (b) November 2002 and (c) June 2003, and for (d) August 2002, (e) November 2002 and (f) June 2003, for Lambert's Bay, South Africa. The dashed lines on each figure represent the 95% confidence intervals, while the values reported to the right of the lags on the y-axis are the autocorrelation coefficients and their standard errors. These figures indicate that microclimate temperatures are predictable from day-to-day in South Africa, but not at Marion Island. Adapted with permission from Deere & Chown (2006).

many populations are responding rapidly to climate change. The most widely reported example of such a response relates to the local colonization and large increases in population numbers and extents of the two

native Antarctic flowering plants (*Deschampsia antarctica* and *Colobanthus quitensis*) over the past four to five decades in the region of the Antarctic Peninsula (Fowbert & Lewis Smith 1994; Lewis Smith 1994;

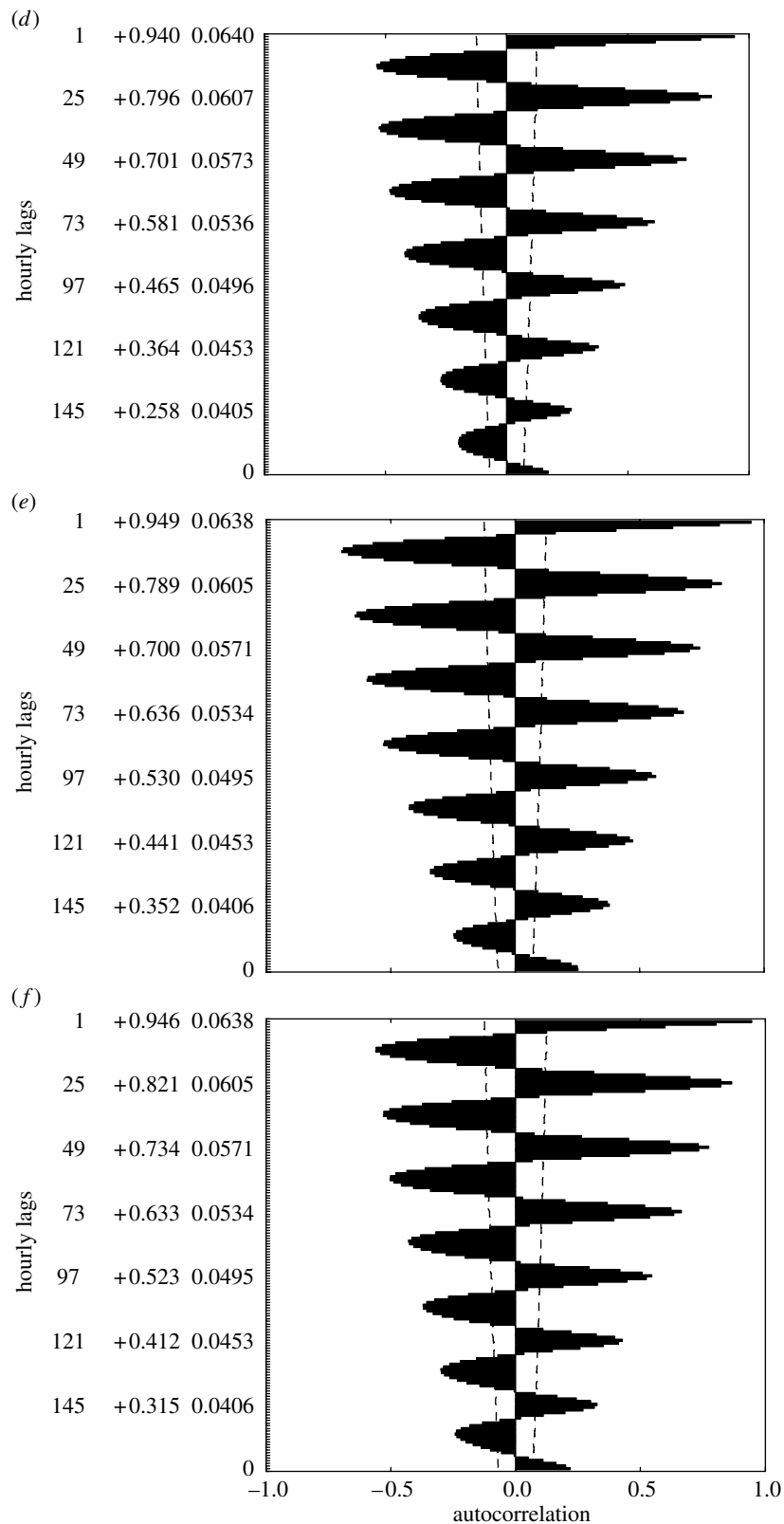


Figure 5. (Continued.)

Grobe *et al.* 1997; Gerighausen *et al.* 2003). Some local populations have increased by two orders of magnitude in as little as 30 years, interpreted as a combination of increased temperature encouraging growth and vegetative expansion, and increased probability of establishment of seedlings. Regional warming is also

thought to increase the frequency of mature seed production (Convey 1996c), and to stimulate growth of dormant seeds in soil propagule banks (McGraw & Day 1997).

Rapid expansions of plant populations on sub-Antarctic Heard Island have been ascribed to warming

(Scott 1990), and this has been implied for changes in the distributions of invasive alien plant species on Marion Island too (Chown *et al.* 2000; see also Frenot *et al.* 2005). Recent manipulative experiments have demonstrated that if the warming and drying trend continues at Marion Island, significant impacts on the keystone cushion plant of fellfields, *Azorella selago*, are likely to be felt (Le Roux *et al.* 2005). Drying increases stem mortality and accelerates autumn senescence. Moreover, shading has a pronounced effect on the plants, reducing their surface integrity, leading to increases in the impacts of mechanical wind stress and a reduction in the capacity of plants to buffer thermal stress and moisture loss. One prediction of the increase in temperatures at the sub-Antarctic islands is that several plant species would overtop the cushions, which often happens in low-altitude areas, so leading to long-term population declines. This kind of effect might be exacerbated by the simultaneous increase in CO<sub>2</sub> levels that are being experienced globally. Elevated CO<sub>2</sub> can offset declining precipitation (stomata need to open less frequently), and is also thought to be responsible for an increase in the abundance of woody plants in many fire-prone areas globally owing to the CO<sub>2</sub>-enhanced growth rates of these woody species (Bond *et al.* 2003). Although interactions between CO<sub>2</sub> and tropospheric ozone effects (Karnosky *et al.* 2003) make predictions of outcomes complex, an increase in woody growth on the islands (woody plants are typically absent from the sub-Antarctic, Lewis Smith 1984) would certainly have significant long-term consequences for *A. selago* and many other species. In this regard, the arrival and establishment of an unidentified woody shrub, far from any sites of human activity, but in the area predicted to receive new natural colonists on Marion Island (Chown & Avenant 1992), is noteworthy, as is the preponderance of woody species on other more temperate Southern Ocean islands such as Gough Island and several of the New Zealand sub-Antarctic islands.

The effects of warming and drying, associated with global climate change, can also be significantly influenced by the presence of invasive alien species. In the case of the sedge, *Uncinia compacta*, a species typical of drier mire vegetation on the Prince Edward Islands, little expansion in response to pronounced declines in precipitation has been found on Marion Island, but considerable expansion has been found on the neighbouring Prince Edward Island (Chown & Smith 1993). This difference is a consequence of invasive alien house mice (*Mus musculus sensu lato*), which are present on Marion Island, but absent from Prince Edward Island. Mice remove seed from individual *U. compacta* plants, so reducing the rate of spread of the population. At the Kerguelen archipelago, eradication of invasive rabbits (*Oryctolagus cuniculus*) has not led to the expected rapid recovery of indigenous plant species favoured by the rabbits largely owing to the effects of drought on the plants (Chapuis *et al.* 2004). By contrast, invasive alien plant species, such as the dandelion *Taraxacum officinale*, have shown substantial increases in abundance.

Increases in house mouse populations, associated with the warming climate at Marion Island (Van Aarde *et al.* 1996), have also significantly impacted indigenous invertebrates, especially the flightless moth, *P. marioni*

and several weevil species which are among the preferred prey of the mice (Gleeson & van Rensburg 1982). Thus, between 1976/1977 and 1996/1997, the biomass of the caterpillars of the moth declined significantly, from  $802 \pm 305$  to  $47 \pm 316$  mg m<sup>-2</sup>, in tussock grassland. Over the same period and in the same habitat, biomass of larvae of the weevil *E. similis* declined from  $375 \pm 83$  to  $45 \pm 34$  mg m<sup>-2</sup> (Chown *et al.* 2002). These impacts have indirectly influenced the abundance of lesser sheathbills (*Chionis minor*), which rely on invertebrates for overwinter survival (Huysen *et al.* 2000). Mice have also led to a long-term change in weevil body size on the island, whereas body sizes and populations appear to be more stable on neighbouring Prince Edward Island. Similar interactions between indigenous and invasive species characterize many other sub-Antarctic islands (Chevrier *et al.* 1997; Chown & Block 1997; Ernsting *et al.* 1999), and changes in climates seem set to exacerbate them (Kennedy 1995a; Walther *et al.* 2002).

### (c) Species level

Temporal variation at the species level amounts either to anagenetic change in one or more populations, to cladogenesis, to hybridization or to some combination of these processes through time (Erwin & Anstey 1995). They can all lead to speciation, and hybridization might also result in the merging of lineages that were becoming distinct so leading to reticulate evolution. Nonetheless, it is also important to recognize that at the species level, large intervals might pass where stasis, rather than change, is the norm, despite complex geographical structure in phenotypic variation (Eldredge *et al.* 2005).

By contrast with Antarctic marine species (Bargelloni *et al.* 2000; Page & Linse 2002), stasis and change in terrestrial taxa have not been well investigated. On the continent, phylogenetic work based on morphological characters has suggested patterns of speciation for paleoendemic taxa such as the continental ameronothroid genus *Maudheimia* (Marshall & Coetzee 2000). On the sub-Antarctic islands, investigations of patterns of speciation have mostly been restricted to the *Ectemnorhinus* group weevils, again largely based on morphological studies, though complemented by ecological and molecular investigations in a few cases (Chown 1990b; Grobler *et al.* 2006). One recent study has also investigated patterns in speciation in the springtail genus *Cryptopygus* (Stevens *et al.* 2006). Comprehensive phylogenetic assessments of taxa, using modern molecular methods, and incorporating ecological and biogeographic information, are curiously rare in the literature on Antarctic terrestrial biodiversity. Springtail sequences have been used to inform broader systematic questions (Frati & Dell'Ampio 2000; D'Haese 2002), and only two recent studies have sought to investigate patterns of speciation across the Antarctic (Allegrucci *et al.* 2006; Stevens *et al.* 2006; §2b)

### (d) Assemblage and ecosystem levels

Antarctic and sub-Antarctic assemblages have changed dramatically over the long term as is clear from the fossil record, and from palynological analyses that provide information on change at scales of several



thousand years (Barnes *et al.* 2006; Cromer *et al.* 2006; Hodgson & Convey 2006). In both the maritime Antarctic and sub-Antarctic, clear successional changes associated with glacial retreat, both in the past and in the present, have been documented, and form among the clearest examples of temporal variation in assemblages (Frenot *et al.* 1998; Lewis Smith 2000). Over the shorter term, changes in the distribution of biogeographically unusual plant assemblages on heated ground provide further evidence that assemblages in the Antarctic are temporally dynamic (Convey *et al.* 2000a). Perhaps of most interest recently are the outcomes of experiments designed to assess the probable impacts of forecast regional climate change on Antarctic communities.

Early studies, using passive greenhouses (or cloches) demonstrated a remarkable effect of warming, including the development of substantial bryophyte assemblages and invertebrate communities on what were previously either unoccupied sites, or sites characterized by low abundance and species richness (Kennedy 1994; Convey 2003a,b). These experiments showed that viable propagules are available in the Antarctic soil, and that strong responses to temperature take place. However, not all treatments have resulted in changes to local assemblages (Sinclair 2002), and passive greenhouse methods have also been criticized for introducing confounding effects and for not replicating the predictions of general circulation models (GCMs) particularly well (Kennedy 1995b). That the GCMs are unable to predict current warming in the Antarctic Peninsula region (King *et al.* 2003) perhaps somewhat ameliorates this critique, but the latter has drawn attention to the need to carefully evaluate the effects of passive greenhouses.

Subsequent manipulations have become more elegant, and have altered temperature, water availability and ultraviolet radiation, and examined their direct effects as well as interactions between them (Day *et al.* 1999). For example, the effects of climate alteration on microarthropod assemblages were investigated in a sophisticated manipulation of vegetation dominated by *D. antarctica* and *C. quitensis* at Anvers Island (Convey *et al.* 2002). Elevated temperatures typically reduced arthropod abundances, which are thought to be a result of increases in water stress owing to increased evaporation. By contrast, enhanced water availability elevated abundances. Microarthropods are known to be especially sensitive to desiccation and this is true also of Antarctic species (Harrisson *et al.* 1991). Filtering of UV-B radiation resulted in an increase in arthropod abundances, and it is thought that the negative effects of UV are associated with indirect effects on the species via changes in resource quality and habitat structure. Similar negative responses to warming and drying have been reported for arthropod communities occupying *A. selago* on Marion Island (McGeoch *et al.* 2006).

#### 4. CONCLUSIONS AND IMPLICATIONS

Variation over several spatial and temporal scales is as much a major characteristic of biodiversity in the Antarctic as it is of biodiversity elsewhere. This is

clearly one of the primary messages that has emerged from both recent and earlier work in the region. Nonetheless, while patterns and mechanisms at some scales (e.g. the plot scale over a few years) are reasonably well understood, and information on variation in biodiversity is becoming available at several other scales, interactions between levels in the genealogical and ecological hierarchies, and by implication different spatial and temporal scales, have received little attention. How processes at different scales cascade up or down the hierarchies to affect each other in terrestrial Antarctic systems is not yet clear. Even so, recent work provides a tantalizing glimpse of the kinds of interactions that might be taking place. Two examples serve to illustrate the point.

On Marion Island, it has long been known that caterpillars of the flightless moth *Pringleophaga marioni* are abundant in recently abandoned (and presumably in occupied) albatross nests, and elevated nutrient availability was typically considered the cause thereof (Joly *et al.* 1987). However, what has now emerged is that these caterpillars are susceptible to repeated low-temperature stresses (i.e. temperatures below their chill coma temperature of  $-0.6^{\circ}\text{C}$ ), and show reduced growth probably as a consequence of reversible gut injury (Sinclair & Chown 2005b). In consequence, any circumstance that reduces this stress should either favour caterpillars or be favoured by them. Occupied wandering albatross (*Diomedea exulans*) nests have thermal regimes approximately  $5^{\circ}\text{C}$  warmer than the surrounding soil environment. Thus, the birds not only reduce the chances of low-temperature stress for the caterpillars, but also provide an environment close to the optimum for caterpillar feeding. They are, in effect, thermal ecosystem engineers (Sinclair & Chown 2006). In consequence, caterpillar biomasses are much higher and much less variable in wandering albatross nests than in surrounding habitats. What this means is that caterpillar physiology and albatross abundance are interacting to provide spatially complex patterns in caterpillar biomass that might well indicate an underlying system of source-sink dynamics.

Physiological and life-history investigations have also demonstrated that invasive alien species have shorter life cycles, steeper rate-temperature relationships and improved physiological performance under warm conditions by comparison with their indigenous counterparts (Barendse & Chown 2000; Chown *et al.* 2002; Slabber *et al.* 2007). In consequence, regional changes in climate, a consequence of global scale change, are likely to have pronounced effects on the relative abundances of invasive alien and indigenous species via differential thermal responses of these two groups of organisms (Frenot *et al.* 2005). Given that similar interactions have been recorded in other systems (Stachowicz *et al.* 2002), it seems probable that interactions between climate change and invasion, often mediated through differing physiological responses, will have major influences on terrestrial systems.

These examples illustrate the significance of investigating variation in diversity across a range of spatial and temporal scales. Only by understanding how processes operating at a variety of scales interact can variation in biodiversity be fully comprehended. In this

context, it is concerning that at several scales even the patterns of variation, let alone their probable underlying mechanisms and interactions, are poorly understood. At the broadest scale, much of the ice-free land that constitutes only 0.32% of the Antarctic continent has yet to be surveyed. Moreover, even in well-known accessible areas, long-term assessments of changes in terrestrial biodiversity (or some component thereof) are either typically not systematically conducted or coordinated, or in some instances where this has taken place (Quayle *et al.* 2002, 2003), have since been abandoned. Without spatially and temporally explicit information on biodiversity, the conservation thereof is simply not possible.

The benefits of spatially explicit conservation planning are widely appreciated (Margules & Pressey 2000) and several conservation programmes are now reaping substantial rewards from their implementation (Younge & Fowkes 2003). Moreover, the importance of temporally explicit information has been highlighted by the discovery of population declines in what were otherwise thought to be abundant British bird species (Vickery *et al.* 2004), and by the establishment of the 2010 biodiversity targets (Balmford *et al.* 2005). In the Antarctic, modern conservation practice has profited taxa such as land-breeding pelagic birds (Woehler *et al.* 2001). However, for some reason, the value of explicit conservation planning and monitoring, and the need for sound species and population-level data to do so have not been fully realized for terrestrial systems, despite early demonstrations of the utility thereof (Usher & Edwards 1986). Two examples, among many, serve to re-emphasize and demonstrate the value of explicit conservation planning in the region.

First, it has been shown that the use of spatially explicit biodiversity data and optimization software can readily identify a set of sub-Antarctic islands that maximize the representation of indigenous species, while minimizing the occurrence of alien species, so improving the longer-term prospects for conservation (Chown *et al.* 2001). Second, recent surveys of Cape Hallett have demonstrated that the diverse arthropod fauna and the Adélie penguin (*Pygoscelis adeliae*) colony are spatially separated, with the algal flats at the site representing primary habitat for many of the species, and the penguin colony being totally devoid of arthropods (Sinclair *et al.* 2006). However, recent changes to the protected area at Cape Hallett have moved the emphasis to protection of breeding birds at the site, and shifts in the recommended campsite are also likely to mean significant disturbance to the flats (<http://www.cep.aq/apa/aspa/sites/aspa106/index.html>). Explicit conservation planning, incorporating all biodiversity elements, would have circumvented the present situation, which now contradicts the original purpose of the protected area.

In conclusion, it is clear that if conservation is to be successful in the Antarctic, then the bodies that guide conservation actions in the region are going to have to keep pace with conservation best practice, and to that end substantial investment in biodiversity research will be required. By comparison with the overall costs of Antarctic research and logistics, this work is inexpensive (Balmford & Gaston 1999). Moreover, the outcomes

thereof will not only inform global understanding of biodiversity, but also contribute to the long-term conservation of Antarctica as a continent for peace and science.

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