ANTARCTIC ECOSYSTEMS

An Extreme Environment in a Changing World

Edited by
Alex D. Rogers
Nadine M. Johnston
Eugene J. Murphy
Andrew Clarke

WILEY-BLACKWELL

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

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Originating from a Theme Issue published in *Philosophical Transactions of the Royal Society B: Biological Sciences.*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

WILEY-BLACKWELL

A John Wiley & Sons, Ltd., Publication

This book was originally published as an issue of the *Philosophical Transactions of the Royal Society B: Biological Sciences* (Volume 362, Numbers 1477/January 29, 2007 and 1488/December 29, 2007) but has been materially changed and updated.

Blackwell Publishing was acquired by John Wiley & Sons in February 2007. Blackwell's publishing program has been merged with Wiley's global Scientific, Technical and Medical business to form Wiley-Blackwell.

Registered office: John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial offices: 9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

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Library of Congress Cataloging-in-Publication Data

Antarctic ecosystems : an extreme environment in a changing world / edited by Alex D. Rogers ... [et al.].
p. cm.
"Originally published as an issue of the Philosophical Transactions of the Royal Society B: Biological Sciences (Volume 362, Numbers 1477/January 29, 2007 and 1488/December 29, 2007) but has been materially changed and updated."
Includes index.
ISBN 978-1-4051-9840-0 (cloth)
1. Ecology–Antarctica. 2. Biotic communities–Antarctica. I. Rogers, Alex, 1968-
QH84.2.A582 2012
577.0998′9–dc23

2011037209

A catalogue record for this book is available from the British Library.

Set in 9/11pt PhotinaMT by Thomson Digital, Noida, India

1 2012

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INTRODUCTION

ANTARCTIC ECOLOGY IN A CHANGING WORLD

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1 INTRODUCTION

Antarctica offers an unrivalled natural laboratory for fundamental research on the evolutionary processes that shape biological diversity on both local and regional scales. Physiologists and ecologists have long been attracted to environments that lie at the limits of the physical conditions capable of supporting life. This is because the polar regions, the deep-sea, hot springs or hydrothermal vents demand striking adaptations at the molecular, cellular or whole-organism level to allow organisms living there to survive, grow and reproduce. Early work on these systems tended to concentrate on specific adaptations, such as membrane function in high-temperature microbes, or antifreeze proteins in polar fish. These specific adaptations are aspects of environmental adaptation in general (Clarke, 1983, 1991; Hochachka & Somero, 2002), and hence the comparative approach has contributed to our overall understanding of evolutionary adaptation at the molecular level. In addition the recent revolution in molecular techniques, particularly those in transcriptomics and proteomics over the past decade, has allowed us to link the genome to the environment in entirely new ways (Feder & Mitchell-Olds, 2003; Chen *et al.*, 2008). For example it is now possible to couple data on protein structure and gene expression to ecosystem-level processes, and thereby to the evolution of entire communities (Whitham *et al.*, 2006). This brings with it the implicit recognition that these links operate over a range of scales of both time and space.

The isolation of the Antarctic continent following the break-up of Gondwana and the subsequent establishment of the Antarctic Circumpolar Current (ACC) and its associated oceanographic regime in the Early Cenozoic have meant that the recent evolution of both the marine and terrestrial biotas has taken place relatively undiluted by biotic exchange. The dramatic climatic changes that characterize the period since the Late Mesozoic have caused major shifts in the composition of both the marine and terrestrial biotas (Clarke & Crame, 1989, 1992, 2010; Chown & Convey, this volume; Rogers, this volume), and the present extreme environmental conditions provide powerful insights into how physiology affects ecology. Finally, the rapid recent regional climate change along the Antarctic Peninsula is already having a strong effect on the physical environment, with biological signals apparent both in land and in the sea (Chown & Convey, this volume; Clarke *et al.*, 2007; Wall this volume; Schofield

Antarctic Ecosystems: An Extreme Environment in a Changing World, First Edition.
Edited by Alex D. Rogers, Nadine M. Johnston, Eugene J. Murphy and Andrew Clarke.

et al., 2010). This is superimposed on ecosystem-level changes that have already been caused by man through overexploitation of marine biotic resources (e.g., Ainley & Blight, 2009) and, in the sub-Antarctic in particular, the introduction of non-native species (Frenot *et al.*, 2005; Convey *et al.*, 2010).

All of these topics have received detailed attention over the past decade or more, but it is only now that the impacts of molecular genomics and new approaches in the study of Antarctic ecosystems at large scales are significantly influencing our understanding of Antarctic ecology and evolution (Clark *et al.*, 2004; Peck *et al.*, 2005). It is therefore timely to synthesize current knowledge by collating invited contributions from key workers in many of the important areas of Antarctic evolution, ecology and ecosystem management. Two unifying background themes provide a framework for this synthesis. The first is climate change, and the second is the importance of spatial, temporal and organizational scale in ecology. The various chapters cover a diverse range of organisms, from microorganisms through marine and terrestrial invertebrates to fish and higher predators, and also a wide array of habitats including deep and continental shelf marine benthos, open-ocean pelagic and terrestrial. Key areas of Antarctica (the western Antarctic Peninsula, East Antarctica, Scotia Sea and Ross Sea) are treated in detail, and topics include physiological adaptation, evolution, biological diversity, trophic interactions and the spatial and temporal structure and operation of ecosystems. Considerable importance has been placed on the historical context and how this influences modern day diversity and biogeography, and also the influence of the latter on management decisions for fisheries and conservation.

2 CLIMATE CHANGE

The Antarctic Peninsula is one of the three areas of the globe that are currently experiencing rapid regional climate change (King, 1994; Vaughan *et al.*, 2003; Ferrigno *et al.*, 2009), the other two being north western North America and an area centred on central Siberia. These are all at high latitude areas and each has experienced a mean annual temperature rise of more than 1.5 K since 1950, compared with a global mean increase of ca 0.6 K.

Although the rapid regional warming of the Antarctic Peninsula has attracted considerable attention (e.g., Turner *et al.*, 2005), it is important to emphasize that for continental Antarctica, significant trends in meteorological temperatures were identified later (Steig *et al.*, 2009). This is because most of the weather stations recording temperatures were from coastal locations around Antarctica and records from West Antarctica were few and discontinuous (Steig *et al.*, 2009). It is only with the development of climate-field-reconstruction techniques that a 50-year spatially complete estimate of temperature anomalies across Antarctica has been achieved (Steig *et al.*, 2009).

The causes of the marked regional warming along the Antarctic Peninsula are not completely understood, although the latest generation of coupled ocean/ice/atmosphere climate models used in the IPCC (Intergovernmental Panel on Climate Change) Fourth Assessment AR4 are able to reproduce the recent warming qualitatively, although with only about half the observed magnitude (Connolley & Bracegirdle, 2007). Recent data have shown a strong correlation between regional atmospheric circulation and air temperature in the Antarctic Peninsula, and it seems likely that an important factor has been a shift towards a more cyclonic atmospheric circulation (Turner *et al.*, 2005). Significant changes have also been observed in sea-ice to the west of the Antarctic Peninsula, where there has been a 40% reduction in annual sea-ice extent over a 26-year period, driven mainly by a reduction in the duration of winter sea-ice (Stammerjohn *et al.*, 2008).

The warming of the atmosphere of the Antarctic Peninsula has had a profound influence on the terrestrial environment. The length of the summer melt period has increased (Vaughan, 2006) and most of the glaciers have retreated during the past 50 years, with the average rate of retreat accelerating (Cook *et al.*, 2005). Glacial retreat in the Peninsula region has been linked to the loss of ice shelves with seven ice sheets having broken up in the past 50 years (Vaughan & Doake, 1996; Ferrigno *et al.*, 2009), including the Wordie Ice Shelf in the 1980s (Doake & Vaughan, 1991) and the middle section of the Larsen Ice Shelf in 2002. Recent studies of aerial photographs and satellite images have confirmed that the retreat of ice shelves over this period along both the western and eastern Antarctic Peninsula is widespread (Ferrigno *et al.*, 2009). While these ice shelf collapses are undoubtedly spectacular, and hence have attracted widespread scientific and public attention, the rapid warming has also led to a significant loss of snow and ice banks, with a consequent increase in the area of open ground.

The rapid regional climatic warming of the Antarctic Peninsula has also been detected in the oceanic system to the west. Meredith and King (2005) have demonstrated a profound warming of the summer ocean surface in the Bellingshausen Sea during the second half of the 20th century (more than 1 K since the 1950s), and a small but significant warming has been detected in the waters of the ACC (Levitus *et al.*, 2000, 2005; Gille, 2002; Barnett *et al.*, 2005). The precise role of the ocean in the regional climate change of the Antarctic Peninsula is unclear, though there is strong evidence for linkage between oceanic processes, sea ice and atmospheric circulation (Yuan & Martinson, 2001; Harangozo, 2006; Ducklow *et al.*, 2007, this volume).

3 THE HISTORICAL CONTEXT

Evidence for the recent rapid regional climate change of the Antarctic Peninsula is based on a relatively short duration of the satellite and instrumental records in Antarctica. In order to place this into perspective a longer historical view is required.

On the geological time-scale, the Antarctic marine environment has cooled from the warm Late Cretaceous to the present polar conditions (Lear *et al.*, 2000; Zachos *et al.*, 2001). Although the overall trend has been one of steadily decreasing temperatures, this smooth trend has been interrupted by episodes of both warming and rapid cooling (Zachos *et al.*, 2001, 2003). On land, the changes in climate and associated glaciations have eradicated almost all the flora and fauna that characterized the Early Cenozoic of Antarctica, driving the evolution of the polar marine and terrestrial biota we observe today (Clarke & Crame, 1989, 1992). There are, however, isolated populations which have been shown by biogeographic and molecular analyses to have been present throughout the Cenozoic glaciations (Chown & Convey, this volume; Convey *et al.*, 2010; Rogers, this volume). The existence of these isolated populations provides an important biogeographic control on reconstructions of the ice sheet through history (Clarke, 2003a; Convey *et al.*, 2009; Convey *et al.*, 2010). Cenozoic climate change has also forced key evolutionary adaptations within species, including changes in morphology, physiology and at the molecular level (Rogers, this volume) allowing species to live at low temperatures. Some of these adaptations, such as the evolution of antifreeze glycoproteins in notothenioid fish, provide some of the clearest examples of environmentally driven macroevolution in the natural world (Chen *et al.*, 1997; Cheng, 1998; Cheng & Detrich, 2007, this volume).

Oceanographic changes around Antarctica, that have been intimately associated with tectonic events associated with the fragmentation of Gondwana, have been critical to this long-term climate change (Clarke & Crame, 1989, 1992, 2010; Rogers, 2007, this volume). Of particular importance were the opening of the Drake Passage between the Antarctic Peninsula and South America, and the Tasman Seaway, which together enabled the onset of the ACC. The precise dating of these events is still a matter of debate, but new isotopic data are starting to constrain the timing (Scher & Martin, 2006). Such oceanographic changes have been critical in the evolution of the Antarctic marine biota and have played a significant role in establishing patterns of marine biodiversity globally (Clarke & Crame, 1989, 1992; Rogers, this volume).

Of more immediate relevance to understanding recent climate change have been the results from sediment cores taken from the Palmer Deep, which reveal variability in the silt-to-clay ratio and microfossil composition at frequencies of between 1800 and 50 years (Leventer *et al.*, 1996). This variability has been interpreted as indicating changes in production linked to the extent of glaciation and long-scale variability in the dynamics of the ACC, notably the extent of the flux of warmer water of the Upper Circumpolar Deep Water onto the continental shelf (Warner & Domack, 2002). Although these data come at present from a limited location, they are important in that they reveal a long history of variability over a range of time scales. They are also critical in that they demonstrate clearly the current rate of regional climate change is unprecedented in the recent geological record (Domack *et al.*, 2005).

4 THE IMPORTANCE OF SCALE

A central theme of the work presented here is the importance of organizational, spatial and temporal scale in Antarctic ecology, from the genome to whole ecosystems, micro-habitats to ocean basins, and seconds to centuries (Murphy *et al.*, 1988). Biological processes are integrated at a range of scales of organization, from the genome to the ecosystem. Climate change has caused large-scale changes at the ecosystem level in Antarctica over geological time-scales (Clarke & Crame, 1989, 1992, 2010; Rogers, 2007, this volume). Recent climate change has also been linked to changes in the distribution, biodiversity and structure of biological communities (Atkinson *et al.*, 2004; Chown & Convey, 2007, this volume; Wall 2007, this volume). Harvesting has also driven changes in the Antarctic ecosystem over the last two centuries and this is discussed below.

The interaction of the environment with the genome of individuals within populations ultimately governs the impact of climate change on communities (Hoffman & Willi, 2008). For organisms unable to shift distribution, the ability to alter gene expression in response to environmental variation at scales from seconds to seasons, or to change the structure and function of proteins over longer time scales in response to climate change, partially dictates the success of species and the composition of biological communities (Feder & Mitchell-Olds, 2003). Such genetic responses to short-term environmental variation or longer-term climatic changes are modified by interspecies (intergenomic) interactions (Whitham *et al.*, 2006). Environmental forcing of evolution, at the extremes of the physical ambit of life, in regions like Antarctica, may constraint adaptation to current and future climate change. This may not only be in terms of tolerance to unfavourable physical conditions, but also in functional limitations on the ability of species to compete successfully or survive predation. For example, terrestrial Antarctic species live in a physical environment characterized by a large variation in physical parameters, and hence the increase in mean temperature associated with climate change may not pose a significant immediate physiological challenge. In contrast, Antarctic marine species have a reduced capacity to tolerate increased environmental temperature, possibly because they have evolved over a long period of time (for at least the past 14–40 million years) to survive stable sub-zero temperatures (Pörtner *et al.*, 2007, this volume). For example, Antarctic icefish have lost the genes encoding for haemoglobin (di Priscu *et al.*, 2002; Cheng & Detrich, 2007), instead relying on direct absorption of oxygen that is in rich supply in cool Antarctic waters. Other notothenioid fish are unable to respond to heat shock via enhanced expression of heat-shock proteins (Hofmann *et al.*, 2000).

Internal processes, such as density-dependent or predator-prey mechanisms, may also play a role in shaping Antarctic communities. These processes can cascade or cross scales and produce effects in which events at one scale have consequences for processes at different scales (Perry and Ommer, 2003). Environmental variability and the continuous cycle of colonization and extinction of communities also influence biodiversity patterns throughout space and time.

To understand how complete ecosystems function and respond to change, we need to be able to integrate interactions between physical, chemical and biological processes across the full range of scales mentioned above. The palaeorecord emphasizes the importance of temporal scale to understanding climate change in Antarctica. However, spatial scale is also important (and the two are, of course, intimately linked; Murphy *et al.*, 2007). Ecologists tend to concentrate on particular groups of organisms or processes, and are thus typically constrained to a particular spatial scale. Thus, microbiologists typically work over spatial scale of 10^{-2}–10^{0} m, benthic and zooplankton ecologists, or terrestrial ecologists typically consider scales of 10^{0}–10^{3} m, whereas ecologists concerned with migratory or widely foraging vertebrates may have to deal with organisms functioning over very wide spatial scales. These scales may differ between marine and terrestrial realms, partly owing to the different role played by physical advection in the two systems. It is important to recognize that the choice of spatial and temporal scale used in ecological studies can constrain understanding of what drives responses to global change (Perry and Ommer, 2003). For example, microbiologists need to consider processes operating over very large spatial scales if they are to understand how their communities are assembled (Marshall, 1996; Marshall & Chalmers, 1997; Marshall & Convey, 1997; Chown & Convey, 2007, this volume; Pearce & Laybourn-Parry, this volume).

5 FISHERIES AND CONSERVATION

Direct impacts of humans on Antarctic ecosystems are perhaps less significant than for much of the rest of the Earth. There have, however, been very marked impacts on the marine ecosystems as a result of over two centuries of harvesting which have followed an almost classic path of exploitation of increasingly lower trophic levels species (*sensu* Pauly *et al.*, 1998). Initially, exploitation was focused on large marine mammals, seals and then the great whales. However, during the second half of the 20th century harvesting of these groups was abandoned due to over-exploitation and the near extinction of populations of Antarctic fur seals (*Arctocephalus gazella*) and several species of great whale. Attention turned to fin fish, the main species of which (marbled rock cod, *Notothenia rossii* and icefish, *Champsocephalus gunnari*) were rapidly exploited to low levels (Ainley & Blight, 2009). In the last few decades fisheries have operated on Antarctic krill, the main prey item of many Antarctic species, and a few finfish species, such as toothfish (*Dissostichus* spp). These patterns of harvesting will have undoubtedly generated major changes in the middle- and upper-trophic level operation of Southern Ocean ecosystems and its consequences will be ongoing. The challenge now, particularly for sustainable management, is to distinguish between the effects of climate-driven change, natural variability (including physical forcing and species interactions), and past and current harvesting on Antarctic ecosystems (Ainley *et al.*, 2007, Croxall and Nicol 2004, Nicol *et al.*, 2007, Murphy *et al.*, 1995). To achieve this requires integrated studies that incorporate both the physical and biological drivers of ecosystem structure and function across a range of scales (Nicol *et al.*, 2007, Murphy *et al.*, 2007).

The management of fisheries has been developed under CCAMLR, which has pioneered an ecosystem-based approach, taking account of interactions within the ecosystem and not just the exploited species. Grant *et al.* (this volume) provide a comprehensive view of the management and conservation issues being considered by CCAMLR. Two particular aspects have developed in recent years to become the focus for future research effort. Firstly, it is now clearly recognized that climate change impacts will need to be included in the next developmental stage of ecosystem-based management. That requires fundamental understanding of the integrated operation of ecosystems and the mechanisms by which climate changes affect components of Southern Ocean ecosystems. The second aspect has been the recognition that, although broad-scale management can maintain the overall sustainability of a fishery on a given species, the localized impacts of fishing could have potentially catastrophic consequences on higher trophic levels species. In the Antarctic predators occur in vast breeding colonies during summer, not just because these are good areas for producing young, but also because their main prey item, Antarctic krill, is plentiful there. These predators are therefore in direct competition with the largest Antarctic fishery. Such concentrated effort is generating major concern and driving a process of setting harvesting controls based on small-scale management units that take account of the localized nature of the resources and ecological interactions. In parallel there has been a focus on the development of methods to protect the marine environment from the effects of fishing, reflecting a shift in global approaches to the ecosystem-based management (EBM) of fisheries. Marine protected areas (MPAs) are an important aspect of such EBM, and scientists and managers are currently considering the potential for protecting regions of the ocean which, for example, may contain important ecosystem processes, may be particularly vulnerable to human impacts or be used as representative areas to distinguish between the effects of harvesting (or other activities) from natural ecosystem changes. The first high seas MPA in the Southern Ocean was implemented in 2009 at the southern shelf of the South Orkney Islands. Development of such networks is seen as an important potential tool for conservation, by allowing sufficient sites to be protected that the whole system can be maintained. Studies of the biodiversity and bioregionalisation within Antarctica are forming an important input into the development of such networks of MPAs (e.g., Brandt *et al.*, this volume; Convey *et al.*, this volume; Grant, this volume). The Agreement on the Conservation of Albatrosses and Petrels (ACAP) also seeks to protect these birds from (among other) impacts of Antarctic fisheries.

Aside from the direct effects of (legal and illegal) fishing on target and non-target species, there are a range of other activities that have affected and continue to affect Antarctic ecosystems and their environment at a range of temporal and spatial scales. These include industrial land-based activities associated with harvesting, introduction of non-native terrestrial species, local impacts such as oil spills from shipping accidents, scientific research and associated logistic operations and tourism. In order to regulate these activities and protect Antarctic ecosystems from their effects a range of instruments and agreements have been developed and considered within and outside the Antarctic Treaty System. These include, for example, the Convention on the Conservation of Antarctic Seals (CCAS), the International Whaling Commission, and agreements under the United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Convention and various national nature reserves and management plans.

Societal recognition of the need to conserve and manage global ecosystems has increased considerably in recent years, in response to awareness of anthropogenic forcing and a rapidly changing climate (Barange *et al.*, 2010). In order for these measures to be successful they must be underpinned by coordinated and integrated international research that provides sound scientific advice on the structure and function of biodiversity and ecosystems and their response to both natural and anthropogenic forcings. Given what we understand of the role of Antarctica in the Earth System so far, stewardship of its distinct ecosystems is of global importance.

6 CONCLUDING REMARKS

The Antarctic has been the focus of a long tradition of fundamental research that provides insights into general ecology. In this volume we have assembled a range of chapters covering Antarctic ecosystems viewed from the perspective of different realms (marine, terrestrial and freshwater), covering different organisms (from microbes, through invertebrates to vertebrates) and integrating across a range of organizational, spatial and temporal scales.

The recognition that parts of Antarctica are experiencing rapid regional climate change provides an unrivalled opportunity to compare ecosystems in a relatively pristine condition (such as the Ross Sea: Smith *et al.*, this volume), at least in terms of climate-induced change, with those (such as the marine system to the west of the Antarctic Peninsula: Clarke *et al.*, this volume; Ducklow *et al.*, this volume) that are changing rapidly. Comparative studies of such systems can provide valuable early insights into the fundamental effects of climate change on biological communities at a range of organizational, temporal and spatial scales. The Antarctic marine environment, although relatively rich and diverse, is not as diverse as many tropical marine environments (Clarke & Johnston, 2003; Gutt *et al.*, 2004; Barnes *et al.*, 2009). This provides an opportunity to study responses to change in a simpler environment than the tropical systems, the oceans of which are expected to bear the brunt of climate change. The knowledge gained through such studies should be applicable to other ecosystems which, owing to high biodiversity and less extreme changes in physical conditions, are more difficult to understand. The relative isolation of the Southern Ocean marine environment (Clarke *et al.*, 2005; Barnes *et al.*, 2006) also means that these responses can be studied independently of any effects of immigration, at least in the short to medium term. Critical to understanding how these marine communities function, and hence underpinning their response to environmental challenges, are the processes of settlement, recruitment and subsequent assemblage development (Barnes & Conlan, 2007). An important limitation here is that our current knowledge of Antarctic marine diversity is limited largely to the continental shelf. Vast areas of Antarctic continental slope and deep-sea remain poorly known (Clarke, 2003b; Clarke *et al.*, 2007). This is, however, starting to change through new sampling programmes that are contributing extremely important new data that will undoubtedly change our understanding of the diversity and evolutionary history of the Antarctic marine benthos (Brandt *et al.*, 2007, this volume).

In contrast to the Southern Ocean marine environment, the Antarctic terrestrial environment is low in diversity and is missing many taxonomic groups (for example, there are only two native species of vascular plant on continental Antarctica). This broad generalisation carries the important caveat that we know relatively little about microbial diversity in Antarctica, and hence we are unable to judge whether this is also low in comparison with elsewhere on Earth. This caveat notwithstanding, the relative simplicity of the Antarctic terrestrial system allows ecologists to probe responses to change at a fundamental level and expose mechanisms that may be obscured in more complex temperate or tropical systems. This is particularly the case when working across scales from the genetic level to communities and ecosystems.

Continuing technological advances in field data collection, modelling, physiology and molecular biology mean that we should expect significant progress in understanding how the Antarctic biota has evolved, how it is distributed and how it will respond to climate and anthropogenic forcings, and the continuing exploitation of biotic resources. Because of the unique structure of governance and management of Antarctic ecosystems we should also be in a strong position to continue and develop scientifically informed sustainable ecosystem-based management of human activities in the Antarctic in the future.

REFERENCES

Ainley, D., Ballard, G., Ackley, S., Blight, L.K., Eastman, J.T., Emslie, S.D., Lescroël, A., Olmastoni, S. Townsend, S.E., Tynan, C.T., Wilson, P. & Woehler, E. 2007 Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? *Antarctic Science* **19** (3), 283–290.

Ainley, D. & Blight, L.K. 2009 Ecological repercussions of historical fish extraction from the Southern Ocean. *Fish and Fisheries* **10**, 13–38.

Atkinson, A., Siegel, V., Pakhomov, E. & Rothery, P. 2004 Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**, 100–103. doi:10.1038/nature02996.

Barange, M., Field, J.G., Harris, R.P., Hofmann, E.E., Perry, R.I., & Werner, F.E. 2010 *Marine ecosystems and global change*. Oxford, UK: Oxford University Press.

Barnes, D.K.A., Hodgson, D.A., Convey, P., Allen, C.S. & Clarke, A. 2006 Incursion and excursion of Antarctic biota: past, present and future. *Global Ecology and Biogeography* **15**, 121–142.

Barnes, D.K.A. & Conlan, K.E. 2007 Disturbance, colonization and development of Antarctic benthic communities. *Phil. Trans. R. Soc. B* **362**, 11–38. doi:10.1098/rstb.2006.1951.

Barnes, D.K.A., Kaiser, S., Griffiths, H.J. & Linse, K. 2009 Marine, intertidal, freshwater and terrestrial biodiversity of an isolated polar archipelago. *Journal of Biogeography*, **36**, 756–769.

Barnett, T.P., Pierce, D.W., AchutaRao, K.M., Glecker, P.J., Santer, B.D., Gregory, J.M. & Washington, W.M. 2005 Penetration of human-induced warming into the world's oceans. *Science* **309**, 284–287. doi:10.1126/science.1112418.

Brandt, A., De Broyer, C., De Mesel, I., Ellingsen, K.E., Gooday, A.J., Hilbig, B., Linse, K., Thomson, M.R.A. & Tyler, P.A. 2007 The biodiversity of the deep Southern Ocean benthos. *Phil. Trans. R. Soc. B* **362**, 39–66. doi:10.1098/rstb.2006.1952.

Chen, Z., Cheng, C.-H.C., Zhang, J., Cao, L., Chen, L., Zhou, L., Jin, Y., Ye, H., Deng, C., Dai, Z., Xu, Q., Hu, P., Sun, S., Shen, Y. & Chen, L. 2008 Transcriptomic and genomic evolution under constant cold in Antarctic notothenioid fish. *Proceedings of the National Academy of Science of the U.S.A.* **105**, 12944–12949.

Chen, L.B., DeVries, A.L. & Cheng, C.-H.C. 1997 Evolution of antifreeze glycoprotein gene from a trypsinogen gene in Antarctic notothenioid fish. *Proc. Natl. Acad. Sci. USA* **94**, 3811–3816. doi:10.1073/pnas.94.8.3811.

Cheng, C.-H.C. (1998) Origin and mechanism of evolution of antifreeze glycoproteins in polar fishes. In: *Fishes of Antarctica: a biological overview* (eds. G. Di Prisco, E. Pisano & A. Clarke). pp. 311–328. Berlin, Germany: Springer.

Cheng, C.-H.C. & Detrich H.W. 2007 Molecular ecophysiology of Antarctic notothenioid fish. *Phil. Trans. R. Soc. B* **362**, 2215–2232.

Chown, S.L. & Convey, P. In press. Spatial and temporal variability across life's hierarchies in the terrestrial, Antarctic. *Phil. Trans. R. Soc. B* **362**. doi:10.1098/rstb.2006.1949

Clark, M.S. *et al.* 2004 Antarctic genomics. *Comp. Funct. Genomics* **5**, 230–238. doi:10.1002/cfg.398.

Clarke, A. 1983 Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Annu. Rev.* **21**, 341–453.

Clarke, A. 1991 What is cold adaptation and how should we measure it? *Am. Zool.* **31**, 81–92.

Clarke, A. 2003a Evolution, adaptation and diversity: Global ecology in an Antarctic context. In: *Antarctic biology in a global context; proceedings of the VIII SCAR biology symposium* (ed. A.H.L. Huiskes, W.W.C. Gieskes, J. Rozema, R.M.L. Schorno, S.M. van der Vries & W.J. Wolff), pp. 3–17. Leiden: Backhuys Publishers.

Clarke, A. 2003b The polar deep seas. In: *Ecosystems of the deep oceans*, vol. 28 (ed. P.A. Tyler), pp. 239–260. Amsterdam, The Netherlands: Elsevier.

Clarke, A. & Crame, J.A. 1989 The origin of the Southern Ocean marine fauna. In: *Origins and Evolution of the Antarctic Biota*, vol. 47 (ed. J.A. Crame). Geological Society Special Publications, pp. 253–268. London, UK: The Geological Society.

Clarke, A. & Crame, J.-A. 1992 The Southern Ocean benthic fauna and climate change: A historical perspective. *Phil. Trans. R. Soc. B* **338**, 299–309.

Clarke, A. & Crame, J.A. 2010 Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Philosophical Transactions of the Royal Society of London, Series B* **365**, 3655–3666.

Clarke, A. & Johnston, N.M. 2003 Antarctic marine benthic diversity. *Oceanogr. Mar. Biol. Annu. Rev.* **41**, 47–114.

Clarke, A., Barnes, D.K.A. & Hodgson, D. 2005 How isolated is Antarctica? *Trends in Ecology & Evolution* **20**, 1–3.

Clarke, A., Griffiths, H.J., Linse, K., Barnes, D.K.A. & Crame, J.A. 2007 How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions* **13**, 620–632.

Clarke, A., Murphy, E.J., Meredith, M.P., King, J.C., Peck, L.S., Barnes, D.K.A. & Smith, R. C. 2007 Climate change and the marine ecosystem of the western Antarctic *Peninsula. Phil. Trans. R. Soc. B* **362**, 149–166. doi:10.1098/rstb.2006.1958.

Connolley, W.M. & Bracegirdle, T.J. 2007 An assessment of IPCC AR4 coupled models. *Geophysical Research Letters* **34**, L22505.

Convey, P., Key, R.S. & Key, R.J.D. 2010 The establishment of a new ecological guild of pollinating insects on sub-Antarctic South Georgia. *Antarctic Science* **22**, 508–512.

Convey, P., Stevens, M.I., Hodgson, D.A., Smellie, J.L., Hillenbrand, C.-D., Barnes, D.K. A., Clarke, A., Pugh, P.J.A., Linse, K. & Cary, S.C. 2009 Exploring biological constraints on the glacial history of Antarctica. *Quaternary Science Reviews* **28**, 3035–3048.

Cook, A.J., Fox, A.J., Vaughan, D.G. & Ferrigno, J.G. 2005 Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science* **308**, 541–544. doi:10.1126/science.1104235

Croxall, J.P. & Nicol, S. 2004 Management of Southern Ocean fisheries: Global forces and future sustainability. *Antarctic Science* **16** (4), 569–58.

di Priscu, G., Cocca, E., Parker, S.K. & Detrich, H.W. 2002 Tracking the evolutionary loss of hemoglobin expression by the white-blooded Antarctic icefishes. *Gene* **295**, 185–191.

Doake, C.S.M. & Vaughan, D.G. 1991 Rapid disintegration of the Wordie Ice Shelf in response to atmospheric warming. *Nature* **350**, 328–330. (doi:10.1038/350328a0)

Domack, E. *et al.* 2005 Stability of the Larsen B ice shelf on the Antarctic Peninsula during the Holocene epoch. *Nature* **436**, 681–685. doi:10.1038/nature03908.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M. & Fraser, W. 2007 Marine pelagic ecosystems: The West Antarctic Peninsula. *Phil. Trans. R. Soc. B* **362**, 67–94. doi:10.1098/rstb.2006.1955.

Feder, M.E. & Mitchell-Olds, T. 2003 Evolutionary and ecological functional genomics. *Nature Revs Genets* **4**, 651–657.

Ferrigno, J.G., Cook, A.J., Mathie, A.M., Williams, R.S., Jr., Swithinbank, C., Foley, K.M., Fox, A.J., Thomson, J.W. & Sievers, J. 2009 Coastal change and glacialogical map of the Palmer Land area, Antarctica: 1947–2009. Pamphlet to accompany Geologic Investigations Series Map I–2600-C2009U. United States Geological Survey, Reston, Virginia, USA.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Stotnicki, M. & Bergstrom, D.M. (2005) Biological invasions in the Antarctic: Extent, impacts and implications. *Biological Reviews* **80**, 45–72.

Gille, S.T. 2002 Warming of the Southern Ocean since the 1950s. *Science* **295**, 1275–1277. doi:10.1126/science.1065863

Gutt, J., Sirenko, B.I., Smirnov, I.S. & Arntz, W.E. 2004 How many macrozoobenthic species might inhabit the Antarctic shelf? *Antarct. Sci.* **16**, 11–16. (doi:10.1017/S0954102004001750)

Harangozo, S. 2006 Atmospheric circulation impacts on winter maximum sea ice extent in the west Antarctic Peninsula region (1979–2001). *Geophysical Research Letters* **33**, L02502.

Hochachka, P.W. & Somero, G.N. 2002 *Biochemical adaptation: mechanism and process in physiological evolution*. Oxford, UK: Oxford University Press.

Hofmann, G.E., Buckley, B.A., Airaksinen, S., Keen, J.E. & Somero, G.N. 2000 Heat-shock protein expression is absent in the Antarctic fish Trematomus bernacchii (Family Nototheniidae). *J. Exp. Biol.* **203**, 2331–2339.

Hoffmann, A.A. & Willi, Y. 2008 Detecting genetic responses to environmental change. *Nature Revs Genets* **9**, 421–432.

King, J.C. 1994 Recent climate variability in the vicinity of the Antarctic Peninsula. *Int. J. Climatol.* **14**, 357–369.

Lear, C.H., Elderfield, H. & Wilson, P.H. 2000 Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science* **287**, 269–272. doi:10.1126/science.287.5451.269.

Leventer, A., Domack, E.W., Ishman, S.E., Brachfield, S., McClennen, C.E. & Manley, P. 1996 Productivity cycles of 200–300 years in the Antarctic Peninsula area: Understanding linkages among the sun, atmosphere, oceans, sea ice, and biota. *Geol. Soc. Am. Bull.* **108**, 1626–1644. doi:10.1130/0016-7606(1996)108!1626:PCOYITO2.3.CO;2.

Levitus, S., Antonov, J.L., Boyer, T.P. & Stephens, C. 2000 Warming of the world ocean. *Science* **287**, 2225–2229. (doi:10.1126/science.287.5461.2225)

Levitus, S., Antonov, J. & Boyer, T. 2005 Warming of the world ocean, 1955–2003. *Geophys. Res. Lett.* **32**, L02604. (doi:10.1029/2004GL021592)

Marshall, W.A. 1996 Biological particles over Antarctica. *Nature* **383**, 680. doi:10.1038/383680a0.

Marshall, W.A. & Chalmers, M.O. 1997 Airborne dispersal of Antarctic terrestrial algae and cyanobacteria. *Ecography* **20**, 585–594. doi:10.1111/j.1600-0587.1997.tb00427.x.

Marshall, W.A. & Convey, P. 1997 Dispersal of mosspropagules in the maritime Antarctic. *Polar Biol.* **18**, 376–383. doi:10.1007/s003000050203.

Meredith, M.P. & King, J.C. 2005 Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.* **32**, L19604. doi:10.1029/2005GL024042.

Murphy, E.J., Morris, D.J., Watkins, J.L. & Priddle, J. 1988 Scales of interaction between Antarctic krill and the environment. In *Antarctic Ocean and Resources Variability* (ed. D. Sahrhage), pp. 120–130. Berlin, Germany: Springer.

Murphy, E. J., Clarke, A., Symon, C. & Priddle, J. 1995 Temporal variation in Antarctic sea-ice – analysis of a long-term fast-ice record from the South-Orkney Islands. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **42**, 1045–1062. doi:10.1016/0967-06 37(95)00057-D.

Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M. P., Thorpe, S., Johnston, N. M., Clarke, A. & Tarling, G. A. 2007 Spatial and temporal operation of the Scotia Sea ecosystem: A review of large-scale links in a krill-centred food web. *Phil. Trans. R. Soc. B* **362**, 113–148. (doi:10.1098/rstb.2006.1957)

Nicol, S., Croxall, J.P., Trathan, P., Gales, N. & Murphy, E. 2007 Paradigm misplaced? Antarctic marine ecosystems are affected by climate change as well as biological processes and harvesting. *Antarctic Science* **19** (3), 291–295.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. 1998 Fishing down marine food webs. *Science* **279**, 860–863.

Peck, L.S. *et al.*, 2005 Genomics: Applications to Antarcticecosystems. *Polar Biol.* **28**, 351–365. (doi:10.1007/s00300-004-0671-8)

Perry, R.I. & Ommer, R.E. 2003 Scale issues in marine ecosystems and human interactions. *Fish. Oceanogr.* **12**: 4/5, 513–522.

Portner, H.O., Peck, L.S. & Somero, G.N. In press. Thermal limits and adaptation in marine ectotherms: an integrative view. *Phil. Trans. R. Soc. B* **362**. (doi:10.1098/rstb.2006.1947)

Rogers, A.D. In press. Evolution and biodiversity of Antarctic organisms: A molecular perspective. *Phil. Trans. R. Soc. B* **362**. doi:10.1098/rstb.2006.1948

Scher, H.D. & Martin, E. E. 2006 Timing and climatic consequences of the opening of Drake Passage. *Science* **312**, 428–430. (doi:10.1126/science.1120044).

Schofield, O., Ducklow, H.W., Martinson, D.G., Meredith, M.P., Moline, M.A. & Fraser, W.R. 2010 How do polar marine ecosystems respond to rapid climate change? *Science* **328**, 1520–1523.

Smith, W.O., Ainley, D.G. & Cattaneo-Vietti, R. 2007 Trophic interactions within the Ross Sea continental shelf ecosystem. *Phil. Trans. R. Soc. B* **362**, 95–111. doi:10.1098/rstb.2006.1956.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C. & Ianunuzzi, R.A. 2008 Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep-Sea Research, Part II* **55**, 2041–2058.

Steig, E.J., Schneider, D.P., Rutherford, S.D., Mann, M.E., Comiso, J.C. & Shindell, D.T. 2009 Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. *Nature* **457**, 459–462.

Turner, J., Colwell, S.R., Marshall, G.J., Lachlan-Cope, T. A., Carleton, A.M., Jones, P.D., Lagun, V., Reid, P.A. & Iagovkina, S. 2005 Antarctic climate change during the last 50 years. *Int. J. Climatol.* **25**, 279–294. doi:10.1002/joc.1130.

Vaughan, D.G. 2006 Recent trends in melting conditions on the Antarctic Peninsula and their implications for ice-sheet mass balance and sea level. *Arctic Alpine Res.* **38**, 147–152. doi:10.1657/1523-0430(2006)038[0147:RTIMCO]2.0.CO;2.

Vaughan, D.G. & Doake, C.S.M. 1996 Recent atmospheric warming and retreat of ice shelves on theAntarctic Peninsula. *Nature* **379**, 328–331. doi:10.1038/379328a0.

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. *Climatic Change* **60**, 243–274. (doi:10.1023/A:1026021217991).

Wall, D.H. In press. Implications of change: Above- and below-ground biotic interactions in a low diversity ecosystem. *Phil. Trans. R. Soc. B* **362**. doi:10.1098/rstb.2006.1950.

Warner, N.R. & Domack, E.W. 2002 Millenial- to decadal scale paleoenvironmental change during the Holocene in the Palmer Deep, Antarctica, as recorded by particle size analysis. *Paleooceanography* **42**, 8004. doi:10. 1029/2000 PA000602.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., Lonsdorf, E.V., Allan, G.J., DiFazio, S.P., Potts, B.M., Fischer D.G., Gehring, C.A., Lindroth, R. L., Marks, J.C., Hart, S.C., Wimp, G.M. & Wooley, S.C. 2006 A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Revs Genets* **7**, 510–523.

Yuan, X. & Martinson, D.G. 2001 The Antarctic Dipole and its predictability. *Geophysical Research Letters* **28**, 3609–3612.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. 2001 Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693. (doi:10.1126/science.1059412).

Zachos, J.C., Wara, M.W., Boharty, S., Delany, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J. & Permoli-Silva, I. 2003 A transient rise in tropical sea surface temperature during the Paleocene-Eocene thermal maximum. *Science* **302**, 1551–1554. (doi:10.1126/science.1090110)

PART 1

TERRESTRIAL AND FRESHWATER HABITATS

CHAPTER 1

SPATIAL AND TEMPORAL VARIABILITY IN TERRESTRIAL ANTARCTIC BIODIVERSITY

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1.1 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; Kreft & Jetz, 2007) 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; Thomas *et al.*, 2008), 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). For example, genetic variation among pinyon pines in resistance to a stem-boring moth, whose feeding activity on susceptible pines can lead to cone elimination, has effects on seed-feeding birds and mammals, and also on fungi in the decomposer community (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 diversity (Brooks *et al.*, 2002; Thomas *et al.*, 2004; Gaston, 2005; Chown & Gaston, 2008; Butchart *et al.*, 2010).

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 restricted mostly to marine systems as a consequence of sealing and whaling (Knox, 1994;

Antarctic Ecosystems: An Extreme Environment in a Changing World, First Edition.
Edited by Alex D. Rogers, Nadine M. Johnston, Eugene J. Murphy and Andrew Clarke.

Trathan & Reid, 2009). Changes to the terrestrial environment were localized in their extent and nature at this time, although this period did see the introductions of many of the alien vertebrates and other groups now present on these islands (Convey & Lebouvier, 2009), and hence the start of their now considerable impacts on ecosystem structure and function (e.g., Chapuis *et al.*, 1994; Bergstrom *et al.*, 2009).

Now the situation is quite different, and both the direct local and indirect influences of humans are increasing across the region (Tin *et al.*, 2009). 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; Convey, 2008; Lee & Chown, 2009), 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 presence of persistent organic and inorganic pollutants in Antarctic systems (Corsolini *et al.*, 2002; Bargagli, 2005; Dickhut *et al.*, 2005), and substantial alterations to terrestrial communities as a consequence of changing climates associated with global warming (Smith, 1994; Bergstrom & Chown, 1999; Walther *et al.*, 2002; Convey, 2003a, 2006; le Roux & McGeoch, 2008). The significance of these impacts, and their scope for increase, given ongoing global change (Archer & Rahmstorf, 2010) and growing human use of the Antarctic (Naveen *et al.*, 2001; Frenot *et al.*, 2005; Tin *et al.*, 2009), have been recognized by the Committee for Environmental Protection of the Antarctic Treaty System (e.g., Mansfield & Gilbert, 2008), 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 likely 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; Chown & Lee, 2009), 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 (Smith, 1984; Convey, 1996a; Vernon *et al.*, 1998). Moreover, very little of the largely ice-covered Antarctic continent (0.32% ice free) is available to the terrestrial biota. Even in the areas that can be used, substantial spatial variation in abundance and occupancy exists (Janetschek, 1970; Smith, 1984; Kennedy, 1993). Indeed, it has been clear ever since extensive work on Antarctic terrestrial systems commenced that they are highly variable both through 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; McGeoch *et al.*, 2008). However, how and why this variation changes with spatial and temporal scale 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 today) has tended to focus on certain areas, species and scales. For example, whilst Antarctic terrestrial biodiversity and the biogeography thereof have been 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; Hodgson *et al.*, 2010). Moreover, no comprehensive database of the distributions of Antarctic and sub-Antarctic species yet exists (see Griffiths *et al.*, 2003 for a marine example). Several non-digital compilations have now been published (e.g., Pugh, 1993; Bednarek-Ochyra *et al.*, 2000; Øvstedal & Smith, 2001; Pugh *et al.*, 2002; Pugh & Scott, 2002; Ochyra *et al.*, 2009), and spatially explicit data used by some of these sources and obtained from elsewhere are now becoming available online (http://data.aad.gov.au/aadc/biodiversity/). However, coverage of ice-free areas remains limited and diversity largely reflects survey effort (see Figure 1.1).

Likewise, quantitative ecological work was, until relatively recently, restricted largely to several maritime and sub-Antarctic islands (see Smith, 1984; Block, 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