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Introduction. Antarctic ecology from genes to ecosystems: the impact of climate change and the importance of scale

Antarctica offers a unique natural laboratory for undertaking fundamental research on the relationship between climate, evolutionary processes and molecular adaptation. The fragmentation of Gondwana and the development of wide-scale glaciation have resulted in major episodes of extinction and vicariance, as well as driving adaptation to an extreme environment. On shorter time-scales, glacial cycles have resulted in shifts in distribution, range fragmentation and allopatric speciation, and the Antarctic Peninsula is currently experiencing among the most rapid climatic warming on the planet. The recent revolution in molecular techniques has provided a suite of innovative and powerful tools to explore the consequences of these changes, and these are now providing novel insights into evolutionary and ecological processes in Antarctica. In addition, the increasing use of remotely sensed data is providing a large-scale view of the system that allows these processes to be set in a wider spatial context. In these two volumes, we collect a wide range of papers exploring these themes, concentrating on recent advances and emphasizing the importance of spatial and temporal scale in understanding ecological and evolutionary processes in Antarctica.

Keywords: glaciation; oceanography; extinction; speciation; extremophile

1. INTRODUCTION

Antarctica offers a unique natural laboratory for fundamental research on the evolutionary processes that shape biological diversity, and the relationships between genome function, physiology and ecology. 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. Although these could be set in a more general context of temperature or pressure adaptation (Clarke 1983, 1991; Hochachka & Somero 2002), 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. 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. 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 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; Chown & Convey in press; Rogers in press), 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 already apparent both in land and in the sea (Chown & Convey in press; Clarke *et al.* 2007; Wall in press).

All of these topics have received detailed attention over the past decade or more, but it is only now that the impacts of genomic science are significantly influencing our understanding of Antarctic ecology and evolution (Clark *et al.* 2004; Peck *et al.* 2005). This is therefore an excellent moment to synthesize current knowledge by collating invited contributions from key workers in many of the important areas of Antarctic ecology from the genomic to the ecosystem level.

Two unifying background themes provide a framework for this synthesis. The first is the importance of spatial, temporal and organizational scale in ecology, as exemplified in the title of the volumes (from genes to ecosystems). The second is the climate change. Our aim is not to force all contributions into an intellectual straightjacket, but rather to provide a context for the different papers with the intention that the two volumes together would provide a coherent insight into the current state of important areas of current Antarctic ecology.

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), the other two being northwestern North America and an

One contribution of 8 to a Theme Issue 'Antarctic ecology: from genes to ecosystems. I'.

area centred on central Siberia. These three areas are all at high latitudes and in each of them mean annual temperatures have risen by 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, it is important to emphasize that for continental Antarctica, there is as yet no significant trend in meteorological temperatures. In some locations, the trend is positive (warming) but in others mean atmospheric temperature has cooled, although in no case are these trends statistically significant (Turner *et al.* 2005). The number of locations for which we have sufficient data is rather small, and most are located on the edge of the continent, but it is nevertheless clear that there is a very strong contrast between continental Antarctica and the Antarctic Peninsula in terms of recent climate change.

The causes of the marked regional warming along the Antarctic Peninsula are not completely understood, and the present generation of coupled climate models fail to predict it (even when forcing from greenhouse gases is included; King *et al.* 2003). 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).

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). In addition, the warming has resulted in the loss of seven ice sheets in the past 50 years (Vaughan & Doake 1996), including the Wordie Ice Shelf in the 1980s (Doake & Vaughan 1991) and the middle section of Larsen Ice Shelf in 2002. 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 & King (2005) have demonstrated a profound warming of the summer ocean surface in the Bellingshausen Sea during the second half of the twentieth century (more than 1 K since the 1950s), and small but significant changes have been detected in the waters of the ACC (Levitus *et al.* 2000, 2005; Gille 2002; Barnett *et al.* 2005).

3. THE HISTORICAL CONTEXT

The relatively short duration of the satellite and instrumental records in Antarctic emphasizes the importance of the longer historical view for placing the recent rapid regional climate change in perspective.

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 effectively eradicated 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). They have also forced key evolutionary adaptations within species, such as antifreeze glycoproteins in fish (Chen *et al.* 1997; Cheng 1998; Cheng & Detrich in press).

Critical to this, long-term climate change have been oceanographic changes around Antarctica, themselves related intimately to tectonic events associated with the fragmentation of Gondwana (Clarke & Crame 1989, 1992; Rogers in press). 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).

Of more immediate relevance to understanding recent climate change has 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 in these two volumes is that biological processes are integrated at a range of scales of organization, from the genome to the ecosystem level. Climate change has caused large-scale changes at the ecosystem level in Antarctica over geological time-scales (Clarke & Crame 1989, 1992; Rogers in press) and in the present day is already manifest in changes in the distribution and structure of biological communities in Antarctica (Atkinson *et al.* 2004; Chown & Convey in press; Wall in press). However, ultimately it is the interaction of the environment with the genome of individuals within populations that governs the impact of climate change on communities. 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, dictates the composition of biological communities. Environmental forcing of evolution, at the extremes of the physical ambit of life, acts as a constraint of adaptation to climate change in the present. This is not only in terms of resistance 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 increased 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 as a trade off for adaptation to constant cold conditions (Pörtner *et al.* in press). Loss of genes (e.g. haemoglobin in icefish) or the ability to upregulate gene expression (e.g. hsp70 in some notothenioids; Hofmann *et al.* 2000) may result in a reduced capacity to function at increased temperatures.

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 ecologists, partly owing to the different role played by physical advection in the two systems. Nevertheless, even 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 in press). To understand how complete ecosystems function, we need to be able to integrate processes and interactions across the full range of spatial and temporal scales.

5. THIS ISSUE

In these two special issues of *Philosophical Transactions of the Royal Society*, we have assembled a range of papers 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 first volume deals primarily with the Antarctic marine environment, which although relatively rich and diverse, is not as diverse as many tropical marine environments (Clarke & Johnston 2003; Gutt *et al.* 2004). Critical to understanding how these marine communities function are the processes of settlement, recruitment and subsequent assemblage development (Barnes & Conlan 2007). Our current knowledge of Antarctic marine diversity is currently limited largely to the continental shelf, and the vast areas of Antarctic continental slope and deep-sea remain poorly known (Clarke 2003). This is, however, starting to change rapidly through new sampling programmes which 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).

The final group of papers in the first volume deals with whole ecosystems viewed at a fairly large spatial scale. Two papers deal with contrasting regional marine ecosystems. Ducklow *et al.* (2007) examine the West Antarctic Peninsula, a marine ecosystem that is experiencing rapid regional climate change and where biological responses are already evident. In contrast, Smith *et al.* (2007) describe the Ross Sea, a system that remains relatively untouched by climate change. The final two papers take very broad-scale views. Murphy *et al.* (2007) review the role of large-scale connections in the operation of the Scotia Sea ecosystem, and Clarke *et al.* (2007) review the effects of recent climate change on the marine system of the Antarctic Peninsula.

The second volume covers the terrestrial and freshwater environments of Antarctica, explores the links between genome and the environment, and examines the influence of human activities on the Antarctic biota.

6. CONCLUDING REMARKS

The Antarctic has a long tradition of fundamental work that provides insights into general ecology. 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), at least in terms of climate induced change, with those (such as the West Antarctic Peninsula) that are changing rapidly. Studying such systems provides valuable early insights into the fundamental effects of climate change on biological communities at a range of organizational, temporal and spatial scales. 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. Technological advances in modelling, physiology and molecular biology mean that we should expect significant progress in understanding how the Antarctic biota has evolved and how it will respond to climate change by the time the field covered in this issue of *Philosophical Transactions of the Royal Society* is reviewed again.

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