

## New terrestrial biological constraints for Antarctic glaciation

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**Summary** Ice sheet modelling of Antarctica supports a generally accepted view that most, if not all, currently ice free ground would have been obliterated at the LGM or previous maxima. However, several recently emerged and complementary strands of biological research cannot be reconciled with this reconstruction of Antarctic glacial history, and therefore challenge the existing paradigm. In this review, we summarise and synthesise evidence across these lines of research. This evidence points to large elements of the contemporary Antarctic terrestrial biota having a long continuous, but isolated, history within the region. These examples relate to all timescales relevant to Antarctic continental evolution (Gondwana breakup to Holocene), and are spatially distributed across much of the continent.

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### Introduction

Several recently emerged and complementary strands of biological research cannot be reconciled comfortably with reconstructions of Antarctic glacial history, challenging the existing paradigm. Here, we summarise and synthesise evidence across these lines of research. The evidence emerging points to large elements of the contemporary Antarctic terrestrial biota having a very long continuous, but isolated, history within the region, and considerably longer than would fit with the current paradigms of glacial ice thickness and extent. At one extreme, several examples point to elements of the extant biota being *in situ* on multi-million year timescales (back to pre-Gondwana breakup), while other examples describe communities developed over Miocene-Pleistocene timescales and, at the youngest extreme, further examples relate to Pleistocene glacial cycles. As well as being drawn across all the timescales relevant to Antarctic continental evolution, disagreement between biological evidence and glacial cycle models is wide-scale, as the sites where very old biological communities are found exist from across the entire continent. We postulate that the biological conclusions have fundamental implications for the understanding of Antarctic glacial history.

### The biological implications of Antarctic glacial history

Antarctica is a continent locked in ice, with 99.7% of current terrain covered by permanent ice and snow, and clear evidence that, as recently as the Last Glacial Maximum (LGM), as well as during earlier periods of glaciation, ice sheets were both thicker and much more extensive than they are now (Sugden et al., 2006). Contemporary terrestrial ecosystems are generally small and isolated, hosting low levels of biological diversity of what are often seen as insignificant groups of small to microscopic invertebrates, lower plants, and microbes (Adams et al., 2006; Convey, in press). Ice sheet modelling of both LGM and previous ice maxima across the continent gives broad support to a general perception that most, if not all, currently ice free ground would have been obliterated at glacial maxima (Huybrechts, 1993, 2002). This underlies a widely held view that all Mesozoic (pre-glacial) terrestrial life of Antarctica was wiped out by successive and deepening glacial events. The conclusion of such destruction is that most, possibly all, contemporary terrestrial life has colonised the continent during subsequent interglacial periods of ice retreat.

Successive ice sheet extension events over Miocene and Pleistocene timescales obscure or destroy evidence of previous boundaries and surface elevations (Florindo et al., 2003; Smellie et al., in press). For much of the continent there are no estimates for previous ice sheet thicknesses based on observed field criteria (cf. Bentley et al., 2006). Some exceptions exist, in particular the geomorphology of the Dry Valleys of southern Victoria Land supports ice retreat from late Miocene maxima around 10-12 Ma (Sugden et al., 2006), while parts of the Prince Charles Mountains may have been ice-free for at least two million years (Fink et al., 2006). As with much of continental Antarctica, some of these areas have received little or no biological research, and their true significance is yet to be confirmed.

There is fossil evidence, some controversial, for cool temperate and tundra communities surviving on the Antarctic continent until the Miocene, mid-Pliocene or even later (Ashworth and Cantrill, 2004, and references therein). The presence of fossils purported to be the last surviving relicts of the Tertiary pre-glacial Antarctic fauna and flora makes the resolution of this debate a major research priority. After the extinction of these groups, and in the absence of later fossils, the contemporary biota provides a potential and, to date, under-utilised source of information to generate more precise constraints on Antarctic glacial history and reconstruction. However, it has only recently become possible to

exploit this avenue, allowing inferences to be made through a combination of improved distributional and classical biogeographical knowledge, and the application of modern molecular techniques.

There is little current glacial or geomorphological evidence to support the existence of refugial areas occupied by terrestrial biota, other than the post Miocene Dry Valley desert ecosystems, and high mountain ranges not overridden during the LGM. In contrast, the majority of Antarctic terrestrial organisms are known from low altitude, mostly coastal, habitats with communities showing little overlap with either Dry Valley-type or mountain (nunatak) biota, which therefore cannot provide the required refugia (Convey, 2003). In the remainder of this extended abstract we attempt to address this apparent contradiction.

### **Contemporary Antarctic biogeography**

Until recently, insufficient distributional data have been available to permit more detailed analyses of biogeographic patterns. Now that these are starting to be completed (Pugh, 1993; Adams et al., 2006; Peat et al., 2007; Chown and Convey, in press), it is becoming clear that regionalisation in the Antarctic terrestrial biota is greater than was previously realised. The biological boundary between the Antarctic Peninsula and continental Antarctica has only recently been recognised as being analogous in significance to the Oriental/Australasian Wallace Line (Chown and Convey, in press). Only a single 'pan-Antarctic' species of Collembola and no Acari or Nematoda are shared across this boundary (Pugh, 1993; Greenslade, 1995; Maslen and Convey, 2006). This indicates that the East/West Antarctic separation is truly ancient. As well as striking discontinuity, the biotas of both the Antarctic Peninsula and continental (East) Antarctica possess high levels of regional endemism (both at continental and intra-regional scales), strongly supporting a hypothesis of dissimilar and ancient origins. Approximately 50% of Antarctic lichen, tardigrade and dipteran species are endemic, along with most mites and springtails, and possibly all nematodes (Pugh, 1993; Greenslade, 1995; Convey and Block, 1996; Andr assy, 1998;  vstedal and Smith, 2001; Convey and McInnes, 2005). Even at the molecular level, recent studies support higher levels of microbial endemism and distinctness than had been thought from previous morphological studies (Boenigk et al., 2006; Taton et al., 2006), again indicating an ancient origin for these taxa. Indeed, 40% of the lichen flora of the remote and young (0.03 – 2 Myr) South Sandwich archipelago consists of species endemic to Antarctica, indicating that the continent itself has been a source of colonizing propagules throughout the Pleistocene (Convey et al., 2000). Some studies have also identified intra-regional endemism and the existence of biodiversity hotspots that were previously unexpected. Thus, the edaphic nematode fauna of Alexander Island shows both much increased species diversity relative to that known elsewhere in the maritime Antarctic, along with a high (40%) proportion of (island) endemic species (Maslen and Convey, 2006). This regional biodiversity hotspot is indicative of a glacial refuge, though its precise location remains unknown, while the limited overlap between the terrestrial arthropod fauna of Alexander Island and the more diverse faunas of Marguerite Bay and the Antarctic Peninsula (Convey and Smith, 1997) precludes this being a refugium for the general maritime Antarctic biota.

Classical biogeographical analyses of distribution patterns have been used to infer evolutionary relationships. Bayly et al. (2003) identified links between continental Antarctic endemic freshwater invertebrates and their nearest known generic relatives from other southern continents tectonically adjacent within Gondwana. The copepod *Gladioferens antarcticus* is a basal species within its subgenus and is known only from freshwater lakes in the Bunge Hills, suggesting that it has not recently reinvaded Antarctica from an extra-continental source. Its congeners are restricted to estuaries of the south coast of Australia and New Zealand, including regions that are adjacent in Gondwanan reconstructions. On a shorter (Pleistocene) timescale, separate populations of the copepod *Boeckella poppei* (also present along the Antarctic Peninsula, Scotia arc and Patagonia) have been shown in palaeolimnological studies to have been present in East Antarctica for > 10,000 years, preceding post-LGM deglaciation of the Antarctic Peninsula, and probably reaching the Prince Charles Mountains during an earlier interglacial (Bissett et al., 2005). Nunatak faunas have been a focus of studies relating to the potential persistence of ancient taxa, forming a specialized, though small, element of Antarctic biodiversity that shows little or no overlap with coastal biotas. The endemic oribatid mite family Maudheimiidae provides a striking example (Marshall and Pugh, 1996; Marshall and Coetzee, 2000), proposed to have continuously inhabited montane regions of East Antarctica at least since the final break-up of Gondwana, with patterns of intra-familial differentiation consistent with Pliocene and Pleistocene glacial episodes.

Critical corollaries of biological endemism and regionalisation are that (1) the general lack of overlap between continental and maritime Antarctic biotas, and between smaller regions within these provinces, and (2) the different classes of ice-free ground and exposure duration described for each province, preclude any one of these elements from acting as a refugium for the biota of another at the LGM or during other earlier periods of complete ice coverage.

### **Dating events in biological history: molecular phylogenetic approaches**

The biogeographical inferences described above provide, ultimately, circumstantial support for the hypothesis of ancient origin for elements of the Antarctic terrestrial biota. Recent developments in methodologies for analyzing molecular phylogeny and phylogeographic tools permit increased understanding of evolutionary relationships and

timescales (Stevens and Hogg 2006a). They have the potential to constrain the dating of significant evolutionary events over a range of timescales. In an Antarctic context such studies have now been applied across timescales from the Pleistocene to the Gondwanan. Mortimer and Jansen van Buuren (2007) have reconstructed phylogeographic relationships across populations of the mite *Eupodes minutus* on sub-Antarctic Marion Island, generating results consistent with both major volcanic events and Pleistocene glacial cycles. Stevens and Hogg (2003), Nolan et al. (2006) and Stevens et al. (2007) have proposed within-species differentiation on timescales of up to c. 1 million years in springtails of Victoria Land. Stevens and Hogg (2006b) have also identified considerably greater divergence rates (x 8) in Victoria Land mites than in springtails – although yet to be explained, if this finding indicates that evolutionary rates have been very different between endemic species, then the timescale for the million-year divergences found in the springtails may be even older. These scenarios are consistent with known periods of glacial expansion and recession.

Deeper timescales received little attention until Stevens et al. (2006) examined the origins of four continental Antarctic endemic springtails in the context of related circum-Antarctic fauna. They inferred recent (< 2 Ma) dispersal/colonization of *Cryptopygus* species between some sub-Antarctic islands, noting a close association between divergence times as estimated by molecular clocks and the geological ages of these islands. In contrast, they found deep (i.e. ancient) divergences between the four continental species, suggesting that they represent a fauna dating from the break-up of Gondwana. Given the levels of isolation identified for Antarctic arthropods, the diversification of these springtail species (21-11 Ma) in ice-free glacial refugia throughout the Transantarctic Mountains was most likely caused by the glaciation of the Antarctic continent during the middle to late Miocene.

A molecular clock approach has been applied to the few chironomid midges indigenous to the Antarctic Peninsula and Scotia Arc (Allegrucci et al., 2006). Two share features that make them key in unravelling the evolutionary history of the region. One (*Belgica antarctica*) is endemic to the Antarctic Peninsula and South Shetland islands, while a close relative (*Eretmoptera murphyi*) is endemic to sub-Antarctic South Georgia – i.e. each species is restricted to an entirely separate regional tectonic element, isolated during the final phases of breaking of the link between southern South America and the Antarctic Peninsula/Scotia Arc (cf. Livermore et al., 2007). Allegrucci et al. (2006) confirm the close relationship between these two species' evolutionary lines, estimating their divergence from each other at c. 49 my, and from more distantly related genera of the same subfamily at c. 68 my. While there are a number of potential inaccuracies within these proposed divergence dates, it is clear that they occurred on a timescale of tens of millions of years, comparable with the geological breakup timescales. Allegrucci et al. (2006) also estimated the timing of separation events between South Shetland and South Georgian populations of a winged chironomid (*Parochlus steinenii*, previously assumed to be a more recent colonist as capable of flight) at c. 7 my. The persistence of such evolutionary lines of terrestrial taxa that are ecologically restricted to low altitude terrestrial and freshwater habitats cannot be reconciled with current reconstructions of Antarctic Peninsula and Scotia Arc glaciation (Convey, 2003).

### Wider implications

The common feature of these various biological findings is that they support the long-term presence of terrestrial biota in terms which cannot simply be reconciled with a widely assumed view of (almost) complete wipe-out associated with successive glacial maxima, either on Pleistocene or longer Neogene timescales. The environmental impacts of glacial cycles and ice sheet advance have indeed rendered most of the contemporary Antarctic terrestrial biota both disharmonic and impoverished, but this does not automatically lead to the conclusion that extinction was followed by post glacial recolonisation of the continent in all or even most major (ordinal/class) taxa. The examples discussed here are geographically dispersed over most parts of Antarctica, involve most of the major extant higher taxonomic groups and carry implications at all of the timescales applicable to the development of Antarctic glaciation. A relictual presence of biota restricted to nunataks is relatively straightforward to understand, at least given the continuous presence of nunataks with appropriate environmental conditions. However, a much greater challenge is presented by other groups of largely low altitude and coastal biota, where acceptance of their relictual nature carries the very clear and fundamentally important corollary of requiring suitable terrestrial habitats to have existed continuously within the region. Furthermore, the degree of intra-Antarctic biogeographic regionalisation that is now identified suggests that the influence of transport (natural dispersal) has been insufficient over time to overcome the processes of evolutionary divergence. Restrictions which biological data impinge on ice sheet or ice stream thickness or extent are potentially highly important, requiring a degree of refinement that is not currently included in reconstructions or models, and demanding that the requirements of the terrestrial biota must be included as constraints in glaciological reconstruction and modelling.

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