

## Biotic interactions in Antarctic terrestrial ecosystems: Are they a factor?

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### Abstract

Antarctic terrestrial ecosystems are noted for their relative simplicity and limited trophic structure. In this context, knowledge of biotic interactions in structuring terrestrial soil communities would seem beneficial from a theoretical perspective as well as from a conservation perspective. Unfortunately, although biotic interactions are generally seen as being insignificant in these unique ecosystems, this view is based upon few explicit studies and very little is known of the role that biotic interactions may play. Accordingly, we review our current understanding of these interactions, including analogues from other appropriate ecosystems. On the basis of this review, we conclude that: (1) Antarctic terrestrial systems are predominantly abiotically-driven systems; and (2) a network of manipulative field and laboratory experiments are needed for establishing any role for biotic interactions in structuring Antarctic soil environments.

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### 1. Introduction

Much of the known biology of Antarctic terrestrial ecosystems is based on species' distributional accounts, and their taxonomic description (e.g. Strandmann, 1967; Wise, 1971). More recent efforts have focused on the physiology, ecology and population genetics of individual species (e.g. Convey, 1994; Courtright et al., 2000; Sinclair et al., 2003; Stevens and Hogg, 2003), and several recent reviews provide coverage of these studies (Convey, 1996, 1997; Beyer and Boelter, 2002; Wharton, 2003; Cowan and Ah Tow, 2004; Bergstrom et al., 2006). Biological knowledge of eastern Antarctica (e.g. Victoria Land), commenced with the early collections made in Northern Victoria Land (approx. 70°S) during the Southern Cross British Antarctic

Expedition (1898–1900) (e.g. Carpenter, 1902), and coverage now extends as far south as 86°37'S (Wise and Gressitt, 1965; Claridge et al., 1971). However, much of this geographic and taxonomic coverage, particularly towards the southern limits, is scant. There are also few detailed autecological studies of Antarctic taxa, and knowledge of any interactions occurring between taxa, is extremely limited throughout Antarctica. For the purposes of this paper, we define biotic interactions as including situations where one (or more) species influence the distribution and abundance of another (after Andrewartha and Birch, 1954; Krebs, 1978). These include “classic” interactions, such as competition, predation, and symbiotic relationships (i.e. mutualism, parasitism, commensalism) as well as processes such as gene exchange, horizontal gene transfer and exoenzyme production (e.g. Cowan, 2000).

Furthermore, as this discussion focuses intentionally on terrestrial soil ecosystems, we restrict our consideration to

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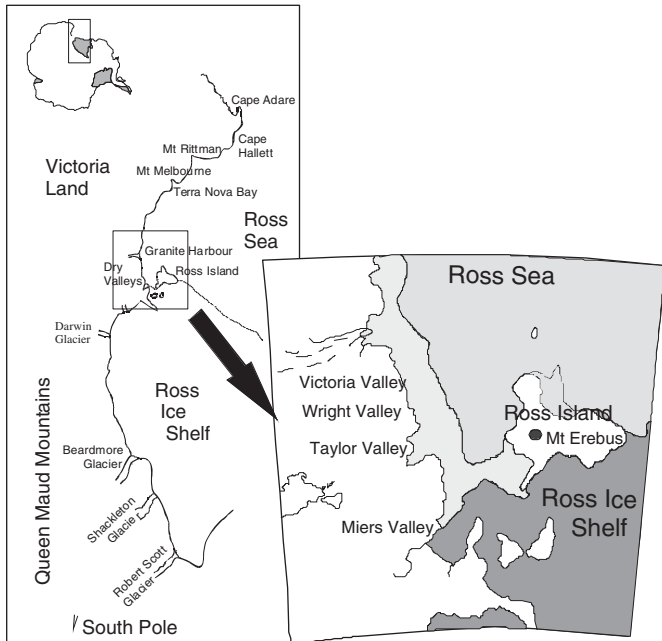


Fig. 1. Map of focus area (Victoria Land and vicinity) showing relative proximity of place names mentioned in the text.

the permanent year-round biota of continental Antarctica and thus do not consider (other than from a nutrient perspective) the megafauna (e.g. penguins, seals, etc.) or the limnetic fauna (e.g. plankton) (Vincent and Vincent, 1982). Accordingly, our coverage includes the bacteria, cyanobacteria, algae, protozoans, plants (lichens, mosses) and invertebrates (e.g. Nematoda, Tardigrada, Rotifera, Acari, Collembola). Although our interest and focus is on eastern Antarctica and Victoria Land in particular (Fig. 1), the paucity of data relating specifically to this region requires that reference be made to analogous systems in Antarctica and elsewhere where appropriate. The following discussion is divided into three sections: (1) overview of the terrestrial environment; (2) current understanding of biotic interactions; and (3) recommendations for future research.

## 2. Overview

Only 0.3% of the Antarctic continent is ice-free today (Fox and Cooper, 1994). Even within these limited ice-free areas (e.g. the Dry Valley deserts of Eastern Antarctica), some biota are further restricted to areas of higher soil moisture (e.g. mosses, arthropods). The Antarctic continent is one of the most physically and chemically demanding environments on earth and was once considered to be adverse to all life (Boyd et al., 1996). The extreme nature of this environment is exemplified in the Antarctic Dry Valley soil ecosystems that experience huge variations in temperature (Doran et al., 2002; Vincent, 1988; Thompson et al., 1971), light regimes, steep chemical gradients, and a high incidence of solar radiation (Dana et al., 1998; Smith et al., 1992). The microbiota inhabiting these ice-free cold desert soil environments are subjected to

excessively low nutrient levels (Vishniac, 1993) and a persistent lack of “bioavailable” water often further compromised by high levels of salinity (Claridge and Campbell, 1977; Bockheim, 1997; Barrett et al., 2004). The additive effects of such extreme aridity and widely fluctuating physicochemical conditions may greatly influence the physiological adaptations and life cycle strategies used by the resident biota.

Early culture-based microbial studies (Cameron et al., 1970; Vishniac and Mainzer, 1972; Vincent, 1988; Wynn-Williams, 1990; McKay, 1993; Friedmann, 1993; Vishniac, 1993) suggested that the soil bacterial diversity and abundance in these cold desert areas was very low, as would be predicted by the extreme nature of the system. This is in stark contrast to nutrient- and water-rich Antarctic ‘ornithogenic’ and fell-field soils, and lake sediments that support vastly higher microbial counts (Sjoling and Cowan, 2003; Ramsey and Stannard, 1986; Wynn-Williams, 1990). It is now well recognized that in most natural systems that culture-based studies under-represent the abundance and diversity of bacteria that are fastidious, co-culture-dependant or are in a viable but non-culturable state (Buckley and Schmidt, 2001; DeLong and Pace, 2001; Rappe and Giovannoni, 2003). In a recent study, ATP analyses were employed to estimate in situ microbial biomass in the surface mineral soils of the Antarctic Dry Valleys (Cowan et al., 2002). These studies revealed that the standing microbial biomass in typical Dry Valley soils is between 3 and 4 orders-of-magnitude higher than in the culture-based estimates. More recently, culture-independent studies employing modern molecular genetic tools suggest that the diversity of Bacteria in these systems may be considerably higher than previously thought (Cowan and Ah Tow, 2004; S.C. Cary, unpublished data), while that of the Archaea is severely diminished and constrained to the globally ubiquitous Group II low-temperature Crenarchaeotes. However, these methods do not discriminate DNA originating from living cells from that supplied by dead cells of legacy DNA.

Freezing temperatures and the periodic absence of moisture may be relatively unimportant for some groups (e.g. bacteria, lichens, algae, protozoa, rotifers, tardigrades, nematodes) due to their possession of stress-resistant or dormant phases, although ecophysiological costs are inevitably involved in the use of these survival tactics (Convey, 2000). Soil moisture and temperature (Moorhead et al., 2002; Frati et al., 1997; Barrett et al., 2004) are likely to be the prime determinants of species occurrences, with most species having similar requirements. Accordingly, the Antarctic environment may be unique in that it could be one of the few examples where abiotic factors (e.g. moisture) are more important than biotic factors (e.g. competition, herbivory, predation) for structuring populations (Convey, 1996). For example, Broady (1984) found that the distribution of algae on the volcanically active Mt Erebus (Fig. 1) was restricted to areas of constant moisture. Similarly, on Mt Melbourne and Mt Rittmann (Fig. 1), hot

water vapour coming from the soil was found to support bacterial and moss growth (Skotnicki et al., 2002; Bargagli et al., 2004). The distribution of nematodes in Taylor Valley (Fig. 1) is structured by soil moisture, carbon and salinity (Courtright et al., 2001; Barrett et al., 2004), although species have differing requirements. For example, *Scottinema lindsayae* occurs in soils of lower soil moisture, higher salinity than does *Eudorylaimus antarcticus* (Barrett et al., 2004) with moisture important for activity (Treonis et al., 2000; Barrett et al., 2004). In the Dry Valleys (Fig. 1), nematodes require a minimum soil-moisture content of >2% to remain in the active (versus anhydrobiotic) state (Treonis et al., 2000). Across the Antarctic, the distribution of the mosses and arthropods (springtails, mites) is clearly restricted to areas of high soil moisture content (Kennedy, 1993; Convey, 2001). It is therefore possible that the co-occurrence of biota is simply a byproduct of the requirement for substrata or habitats with suitable levels of soil moisture, rather than being truly interconnected. To date very few studies have focused on the biological interactions that do occur in Antarctic terrestrial ecosystems (Convey, 1996 reviews the limited evidence for competition and predation in maritime Antarctic invertebrate communities) and virtually no detailed studies have focused on Victoria Land. However, even in the simplest faunal communities so far described (Freckman and Virginia, 1997; Convey and McInnes, 2005), it is known that at least two consumer trophic levels are present—detritivore/microbivore and omnivore/predator.

### 3. Biotic interactions

Despite the lack of studies focusing specifically on biotic interactions, some inferences on potential interactions are possible. For example, bryophytes in drier microhabitats are often colonized by lichens and epiphytic cyanobacteria, and algae (e.g. chlorophytes, diatoms) are associated with moss and liverworts (Green and Broady, 2001). Casual observation suggests that springtails and mites are often found on or in the vicinity of moss beds. This could indicate both a biotic interaction (e.g. moss providing food/habitat) and/or that the abiotic conditions at the site are suitable for both taxa. Several Antarctic taxa are also known to have associations with lichens (e.g. Lindsay, 1978). Based on studies from Antarctica and elsewhere, potential interactions with lichens are likely to include nematodes (Pickup, 1988), rotifers (Pyatt, 1968), tardigrades (Argue, 1971), mites (Seyd and Seaward, 1984) and springtails (Aptroot and Berg, 2004). However, none of these interactions has been specifically studied in Victoria Land.

Predation, and even the more general concept of direct intra- or interspecific competition, is generally thought to be insignificant in Antarctica (Convey, 1996). From simple biodiversity studies it is clear that Antarctic faunal communities include representatives that are either known to be predators or omnivores (e.g. gamasid mites, certain

prostigmatid mite genera, various nematode and tardigrade genera), or belong to families or genera that are characteristically predaceous or omnivorous elsewhere (e.g. springtails of the genus *Friesea* are typically nematophagous, eudorylaimid nematodes are typically omnivorous). Nematode-trapping fungi have also been described from different locations in the Antarctic (Maslen, 1982). The wider fauna of Victoria Land includes examples of most such taxa. However, we caution that in the absence of detailed autecological studies we cannot state categorically that these predaceous interactions indeed take place.

The few detailed studies of predation amongst the Antarctic terrestrial biota that have been published relate to the impacts of predatory mites in the maritime Antarctic (Jumeau and Usher, 1987; Lister et al., 1988; Usher et al., 1989). These studies failed to detect any significant impact of predator activity on prey (springtail) populations across the naturally occurring range of prey densities, in terms of identifying a “functional response” in experimental studies over a range of realistic prey densities. This was interpreted as suggesting that natural predator densities could be comfortably supported by the lowest recorded prey densities in their habitats—in effect, these predators can be seen as “ecological luxuries” in these ecosystems. However, there was also some evidence for competition between predatory mite species in the form of apparent niche shifts in their choice of prey species in the presence/absence of competing predators. Among species indigenous to sub-Antarctic islands, Davies (1987) proposed that competition between two carabid beetles has resulted in non-overlapping adult size distributions where they occur sympatrically in fellfield habitats but that where they occur separately the size distributions overlap. Analyses of body size ratios between different species of weevil on the Prince Edward Islands also seem to provide some evidence of interspecific competition as resident species in some biotopes have size ratios larger than those expected from random (Chown, 1992). Other than these studies, the general assumption of the insignificance of competitive interactions, even within trophic levels, is based on the apparent superabundance of food relative to consumer populations. However, this assumption is based on little hard evidence and it should be recognized that few detailed dietary studies have been attempted for any Antarctic metazoan, while those that have (e.g., Overhoff et al., 1993; Davidson and Broady, 1996; Worland and Lukešová, 2000) have demonstrated considerably greater dietary selection than previously assumed.

Based on these examples, it is possible that biotic interactions may be limited to a few larger taxa (e.g. springtails, mites) and even in these cases, may only be opportunistic rather than obligatory. Ultimately, a reduction in trophic level interaction/dependency will lead to complete de-coupling of trophic structure. In this case, abiotic factors become the primary drivers of the system—a testable hypothesis. To be a specialist in this environment would seem to be maladapted, and we are aware of no

examples of specialization. One of the most interesting findings is that the diversity of bacteria and genetic diversity of arthropods (e.g. Frati et al., 2001; Stevens and Hogg, 2003) is much higher than we would have predicted, begging the question of what is driving the system. Given the potential lack of specialists, are we looking primarily at an abiotically-driven system? Are all trophic levels decoupled, and is there a genuine lack of specialization?

#### 4. Recommendations

To address these questions, we will need to address at least two shortfalls in our current knowledge. Firstly, we really need to know what is there (see also Wall, 2005). In order to understand how the complexity of the system, or any interaction, changes under given environmental conditions, we need to have an accurate knowledge of the species composition of communities. We have a reasonable understanding of the distributions of “larger” life-forms (e.g. mosses, lichens, invertebrates), but even in these cases on closer inspection, diversity is typically under-estimated. For example, a recent, re-survey of the biota in the Mt Kyffin region near the Beardmore Glacier (84°S) found an additional 19 species of lichens—6 previously unknown in the Antarctic (T.G.A. Green, unpubl. data). Given that this is potentially problematic for the eukaryotes, there is a comparative chasm for the prokaryotes. The Antarctic continent has purportedly some of the simplest ecosystems on the planet (Wall, 2005). If we are unable to accurately assess biodiversity here, what are the chances of us being able to assess more complex ecosystems elsewhere? The increasing use and accessibility of molecular techniques (e.g. DNA barcoding, Hebert et al., 2003), may greatly assist in this regard.

Secondly, as in other ecosystems, we need to enhance our technological capacity. There are issues of scale that at present we are ill-equipped to deal with. For example, how do we get to the spatial scale that is relevant to a nematode or a microbe? Collecting soil samples and then separating organic from inorganic material allows determination of species presence/absence as well as co-occurrence. However, it is very difficult to establish biotic interactions (other than associations) at this level. At the temporal scale, several features (e.g. life cycles), are outside the realm of our current experimental capacity. For example, the life cycle of an individual mite or springtail in Antarctica may last five years or more (Convey, 1994, 1996). Antarctic lichens grow very slowly and may increase in size as little as 1 mm in a hundred years (T.G.A. Green, unpubl. data). The dominant nematode in Dry Valley soils, *S. lindsayae* has a life cycle in a laboratory study of >200 days at optimal temperature, but these temperature conditions do not exist in field situations, while development is further limited by the extensive periods spent in anhydrobiosis in these desert soils, suggesting several years may be needed to complete the life cycle (Overhoff et al., 1993).

By addressing these difficult issues, we will be able to focus on observational scales consistent with the processes we are trying to resolve as well as meaningfully pursue issues of biotic interaction. Questions of this nature may be potentially addressed using field and laboratory approaches. Antarctic terrestrial ecosystems, and especially those encountered in the Dry Valleys, are excellent habitats on which to conduct these types of studies: they are dominated by microbes, facilitating the replication of food webs without introducing container effects encountered when ‘bottling’ macro-organisms. Furthermore, species richness and trophic complexity are often exceedingly low, enabling the biological complexity present in nature to be approached and observed in the laboratory or field mesocosm. For example, questions such as the effects of excluding predators from food webs and the influence of biological diversity on fluctuations in food webs can be readily addressed. Combined with the use of food choice experiments, in which a range of microbial prey are offered to predators (Newsham et al., 2004), field and laboratory studies also have the ability to answer fundamental questions about the influence of connectivity in food webs on resilience to perturbation (Pimm, 1984).

Studies of Dry Valley soils have identified that some apparently have no invertebrate biota (e.g. Freckman and Virginia, 1997), while elsewhere in continental Antarctica, individual nunataks (Sohlenius and Boström, 2005) or entire sub-regional faunas (Convey and McInnes, 2005) have been described whose invertebrate component is limited to tardigrades, rotifers and protozoans, lacking the otherwise globally ubiquitous nematodes. Taken together, these locations provide an exceptional opportunity for the study of the assembly rules of the planet’s simplest terrestrial ecosystems. In these instances, field observation employing a comparative approach may be instructive. For example, it may be possible to characterize resource use at a site where one or two species are present and then compare this to locations where additional species are present to examine any evidence of niche shifts.

Whilst the rewards of field and laboratory approaches are potentially high, they also present considerable challenges. For example, there may be difficulties in culturing some organisms required for experimental work (e.g. Newsham et al., 2004). We also face the additional challenge that we are entering a period of unprecedented change for Antarctic ecosystems. What will be the consequences of altered soil temperature profiles and potential expansion (or contraction) of ice-free areas as a consequence of global change (Doran et al., 2002; Turner et al., 2002; Convey, 2003; Wall, 2005)? How might this influence the functioning of existing communities or facilitate the introduction of non-indigenous species (e.g. Rounsevell, 1978) to indigenous communities, or translocations of indigenous species to areas where they are not currently found (Frenot et al., 2005)? To comprehend how Antarctic systems will respond to change, we need to urgently understand the functioning of the current systems

whilst they are intact. To properly understand interactions in these unique systems, we are going to need to embrace an interdisciplinary, international, collaborative effort drawing together global expertise and resources to address these compelling issues. The International Polar Year (IPY) may provide an ideal opportunity to coordinate and focus research efforts thus making more efficient use of available resources.

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