

Antarctic nematode communities: observed and predicted responses to climate change

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Received: 6 December 2010 / Revised: 10 April 2011 / Accepted: 11 April 2011
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Abstract The rapidly changing climate in Antarctica is impacting the ecosystems. Since records began, climate changes have varied considerably throughout Antarctica with both positive and negative trends in temperatures and precipitation observed locally. However, over the course of this century a more directional increase in both temperature and precipitation is expected to occur throughout Antarctica. The soil communities of Antarctica are considered simple with most organisms existing at the edge of their physiological capabilities. Therefore, Antarctic soil communities are expected to be particularly sensitive to climate changes. However, a review of the current literature reveals that studies investigating the impact of climate change on soil communities, and in particular nematode communities, in Antarctica are very limited. Of the few studies focusing on Antarctic nematode communities, long-term monitoring has shown that nematode communities respond to changes in local climate trends as well as extreme (or pulse) events. These results are supported by in situ experiments, which show that nematode communities respond to both temperature and soil moisture manipulations. We conclude that the predicted climate changes are likely to exert a strong influence on nematode communities throughout Antarctica

and will generally lead to increasing abundance, species richness, and food web complexity, although the opposite may occur locally. The degree to which local communities respond will depend on current conditions, i.e., average temperatures, soil moisture availability, vegetation or more importantly the lack thereof, and the local species pool in combination with the potential for new species to colonize.

Keywords Antarctica · Climate change · Community composition · Diversity · Nematode · Precipitation · Soil · Temperature

Introduction

It is generally accepted by the scientific community that climate changes will occur worldwide, but that changes are likely to occur faster and reach greater magnitudes in the Polar Regions (IPCC 2007). Accordingly, the most rapid climate warming to date has been observed in maritime Antarctica, where temperature increases of almost 3°C have been measured over the second half of the twentieth century (Turner et al. 2005). The observed changes in climate in Antarctica do however show high spatial variability, and both increases and decreases in temperature and precipitation have been observed locally. However, a more directional warming and increased rates of precipitation are predicted for the twenty-first century (Steig et al. 2009; Turner et al. 2009).

Antarctic terrestrial ecosystems represent some of the harshest environments on earth (Fountain et al. 1999). The main limit to life in these systems is low temperature, which controls primary productivity and growth and survival rates, and also impairs water availability. This is confounded by low precipitation rates, particularly in

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continental Antarctica, where large areas are considered polar deserts that support only species poor ecosystems (Wall and Virginia 1999; Wall 2005). Even a small increase in temperature and water availability may therefore have a great impact on the biotic communities throughout Antarctica (Convey 2003a; Wall and Virginia 1999).

The terrestrial Antarctic fauna is generally well adapted to the harsh conditions (Block et al. 2009). Such adaptations, including constituent expression of antifreeze proteins (Adhikari et al. 2009, 2010), allow these species to dominate under current climate conditions but adaptations such as this are likely costly trade-offs that would render them less competitive in a gentler climate. These species may therefore be vulnerable to being outcompeted by invasive species that have not evolved such costly adaptations (Bergström and Chown 1999). This is non-trivial, as the rate of successful colonization events is likely to increase in a warmer and wetter Antarctica (Sinclair and Stevens 2006). Although our current knowledge of climate change impacts on Antarctic terrestrial communities is poorly known, it is reasonable to conclude that the predicted warming and increased rates of precipitation could have disproportionately large impacts on Antarctic terrestrial communities (Chapin et al. 2008; Freckman and Virginia 1997).

Here, we provide an overview of the current knowledge of the potential impact the predicted climate changes may have on nematode communities in Antarctica focusing on temperature and precipitation changes. We first introduce Antarctica as a habitat and the nematode communities found in Antarctic soils, then outline how climate has changed in Antarctica since modern records began and consider the predictions for climate change in the twenty-first century. We conclude by showing how these changes have already influenced Antarctic nematode communities and what the future communities may look like based on a literature review including both observational studies and experimental climate manipulations.

Antarctica as a habitat

Antarctica covers an area of about 13 million km² or about 1.5 times the size of the United States. However, because of the very cold climate only c. 0.32% of this area is permanently ice-free (Ugolini and Bockheim 2008). Currently, terrestrial soil fauna have a very limited area of habitat suitable for colonization. Moreover, soil patches are often spatially isolated at scales ranging from meters to hundreds of km (Huiskes et al. 2006), making it difficult for soil animals to disperse between these.

A large part of the present exposed soils on the continent would have been covered by ice during the last glacial maximum, and colonization by soil fauna is, therefore, likely to have occurred relatively recently compared to many other terrestrial ecosystems. Yet some areas, such as part of the MDVs, appear to have been exposed for as long as 12 Ma (i.e., since the Miocene), and some inland nunataks and mountains were not covered even during the Pleistocene glacial maxima (Turner et al. 2009). These long-term exposed soils have thus provided the local fauna with refugia for survival during glacial maxima (Convey et al. 2008; Stevens and Hogg 2003; Stevens et al. 2006).

Antarctica broadly represents three distinct climatic regions: the sub-Antarctic, maritime and continental Antarctica with the sub-Antarctic being the most favorable, and continental Antarctica being the most hostile, environments. The average monthly temperatures reach 5–10°C during summer in the sub-Antarctic, 0–2°C in maritime Antarctica (and temperatures above freezing for 1–4 months), while the average monthly temperature remains below freezing in continental Antarctica (Convey and Smith 2006; Smith 1984). In this paper, we will focus on the terrestrial environments found in maritime and continental Antarctica to limit the geographic and climatic area covered. The maritime Antarctic includes the western side of the Antarctic Peninsula and the islands in its vicinity as well as the islands of the Scotia Arc (South Shetland, South Orkney and South Sandwich Islands) and Bouvetøya, while continental Antarctica comprises the remainder of the continent (Smith 1984; Turner et al. 2009).

The remoteness of Antarctica and weather patterns of the southern ocean has, in combination with the harsh local climate, limited successful colonization events of species from other parts of the world (Convey et al. 2008). Consequently, the terrestrial fauna as well as the flora of Antarctica shows a very high degree of endemism and a restricted diversity due to historical climatic restraints. The diversity of fauna in maritime and continental Antarctic terrestrial ecosystems is therefore limited to about 520 species of invertebrates of which 170 are free-living endemics (Adams et al. 2006; Convey 2008a; Pugh and Convey 2008). Moreover, the plant community is composed of only two species of vascular plants (hairgrass, *Deschampsia antarctica*; pearlwort, *Colobanthus quitensis*, both limited to maritime Antarctica), about 111 moss species (Ochyra et al. 2008) and 273 lichens (Øvstedal and Smith 2009). Although the plant communities can be relatively well developed in the milder parts of Antarctica, they are much more limited or non-existent in continental Antarctica where bare soils are predominant. The terrestrial species diversity follows the climatic pattern, and more

species are found in the gentler maritime climate than in the harsh continental climate.

Current nematode communities of Antarctic terrestrial ecosystems

As for the biota in general, the long-term isolation and harsh climate of Antarctica is reflected by the low number of nematode species currently recognized in Antarctica as well as a high degree of endemism. Historical glaciation events and the current spatial isolation of habitable soils have led to a very patchy distribution of nematode communities and no apparent overlap in nematode species between maritime and continental Antarctica (Adams et al. 2006; Andr ssy 1998; Andr ssy and Gibson 2007; Maslen and Convey 2006; Table 1).

To date, 32 species have been formally recorded in maritime Antarctica compared with 23 species in continental Antarctica (Andr ssy 1998; Andr ssy and Gibson 2007; Kito and Ohyama 2008; Maslen and Convey 2006). However, the taxonomic resolution of many species is still unresolved because identification is difficult for non-specialists (Adams et al. 2006), and there are several instances of misclassifications of Antarctic nematode species (Andr ssy 2008). Consequently, the number of described species probably underestimates the total diversity of nematodes. Similarly, a survey of sites in maritime Antarctica revealed 23 species of nematodes not known to science (Maslen and Convey 2006) and 28 nematode genera new to Antarctica have recently been recorded at Byers Peninsula (Nielsen et al. 2011). Our knowledge of spatial and temporal patterns of nematodes in Antarctica is therefore relatively confined.

Within sites, the species richness is often low and usually represents only a subset of the regional species pool. In conjunction with the gentler climate in maritime Antarctica, some of the highest diversities have been recorded there. For example, 13 and 25 species were recorded in the Marguerite Bay area and in Mars Oasis, respectively (Maslen and Convey 2006), and 37 genera were recorded on Byers Peninsula (Nielsen et al. 2011). However, a large percentage of these represent undescribed species, and hence, our knowledge about species distributions and ecology in maritime Antarctica is limited. In contrast, the MDVs, a polar desert with an average annual temperature of about -20°C and <100 mm precipitation per year (Fountain et al. 1999), is dominated by the nematode *Scottinema lindsayae*. This nematode is the only species that thrives in the predominant dry, saline soils (Adams et al. 2006; Wall and Virginia 1999). Besides *S. lindsayae*, the greater Victoria Land soils with higher soil moisture and greater organic matter content (including the MDVs) is

inhabited by *Eudorylaimus* and *Plectus* (each represented by 3 species), and the nematode *Geomonhystera antarctica* can be found sporadically in moist soils in the MDVs (mainly in southern Victoria Land), while *Panagrolaimus davidi* is mainly found in coastal areas (Adams et al. 2006; Porazinska et al. 2002).

At the landscape scale, higher nematode abundances are associated with vegetated soils (Barrett et al. 2006; Convey and Wynn-Williams 2002; Yergeau et al. 2007), and plant cover has a strong influence on nematode community composition at least when compared with those found in bare soils (Convey 2003b; Yergeau et al. 2007). This is similar to the patterns observed in other ecosystem types. Overall, the nematode communities of Antarctica are considered simple with few species (Wall and Virginia 1999) and show very patchy distributions (Sohlenius and Bostr m 2005). Within Victoria Land in eastern Antarctica, there appears to be a decrease in the species richness of nematodes with increasing latitude and the community composition is related to local environmental characteristics (Barrett et al. 2006). Similarly, it has been shown that nematode community structure changes with latitude (from the Falkland Islands at 51°S to the base of the Antarctic Peninsula at 72°S), although this change does not appear to be directly related to climate variables per se but rather local environmental characteristics (Yergeau et al. 2007).

At the species level, the nematode communities of the MDVs are probably the best studied in Antarctica. Many studies have concluded that these communities are structured mainly by abiotic factors, such as soil moisture and salinity (e.g., Courtright et al. 2001; Poage et al. 2008; Powers et al. 1998), with little evidence for any discernable influence of biotic interactions on the composition of nematode communities (Hogg et al. 2006). However, soil resource legacy effects from deposition of organic material at previous higher paleolake and sea levels (Burkins et al. 2000) and from contemporary fluctuations in lake extents (Elberling et al. 2006) also have a considerable impact on present communities.

Less well explored, but similar patterns have been found for the nematode fauna elsewhere in continental Antarctica. For example, the nematode *Panagrolaimus davidi* tends to be related to nutrient-rich soils often associated with penguin rookeries while *S. lindsayae* occurs at higher-elevation sites in drier and saltier soils at Cape Bird, Ross Island, East Antarctica (Porazinska et al. 2002; Sinclair 2001; Sinclair and Sjursen 2001). A survey of 368 samples collected in a range of microhabitats on 14 nunataks in Dronning Maud Land, East Antarctica, showed that *Panagrolaimus* dominated ornithogenic soils while *Plectus* dominated in mosses (Sohlenius and Bostr m 2008). In contrast to the limited evidence for biotic interaction in Victoria Land (Hogg et al. 2006), there appears to be

Table 1 A list of nematode species formally recorded in maritime and continental Antarctica

Maritime Antarctica	Continental Antarctica
Adenophorea	Adenophorea
Chromadoria	Chromadoria
Araeolaimida	Araeolaimida
Plectidae	Plectidae
<i>Ceratopectus armatus</i> (Bütschli, 1873) Andrásy, 1984 ^a	<i>Chiloptectus masleni</i> Boström, 1997 ^a
<i>Plectus antarcticus</i> de Man, 1904 ^a	<i>Plectus frigophilus</i> Kirjanova, 1958 ^a
<i>P. belgicae</i> de Man, 1904 ^a	<i>P. murrayi</i> Yeates, 1970 ^a
<i>P. insolens</i> Andrásy, 1998 ^a	
<i>P. meridianus</i> Andrásy, 1998 ^a	Chromadorida
<i>P. tolerans</i> Andrásy, 1998 ^a	Hypodontolaimidae
Teratocephalidae	<i>Hypodontolaimus antarcticus</i> Andrásy & Gibson, 2007 ^b
<i>Teratocephalus pseudolirellus</i> Maslen, 1979 ^a	Monhysterida
<i>T. rugosus</i> Maslen, 1979 ^a	Monhysteridae
<i>T. tilbrooki</i> Maslen, 1979 ^a	<i>Geomonhystera antarctica</i> Andrásy, 1998 ^a
Monhysterida	<i>Halomonhystera continentalis</i> Andrásy, 2006 ^b
Monhysteridae	<i>H. halophila</i> Andrásy, 2006 ^b
<i>Eumonhystera vulgaris</i> (de Man, 1880) Andrásy, 1981 ^a	Triplonchida
<i>Geomonhystera villosa</i> (Bütschli, 1873) Andrásy, 1981 ^a	Trobrilidae
Enoplia	<i>Eutobrilus antarcticus</i> Tsalolikhin, 1981 ^a
Dorylaimida	Enoplia
Dorylaimidae	Dorylaimida
<i>Calcaridorylaimus signatus</i> (Loof, 1975) Andrásy, 1986 ^a	Qudsianematidae
<i>Mesodorylaimus chipevi</i> Nedelchev and Peneva, 2000 ^b	<i>Eudorylaimus antarcticus</i> (Steiner, 1916) Yeates, 1970 ^a
<i>M. imperator</i> Loof, 1975 ^a	<i>E. glacialis</i> Andrásy, 1998 ^a
<i>M. masleni</i> Nedelchev and Peneva, 2000 ^b	<i>E. nudicaudatus</i> Heyns, 1994 ^a
<i>M. antarcticus</i> Nedelchev and Peneva, 2000 ^b	<i>E. shirasei</i> Kito et al., 1996 ^a
Nordiidae	Secernentea
<i>Enchodelus signyensis</i> Loof, 1975 ^a	Rhabditia
<i>Rhysocolpus paradoxus</i> (Loof, 1975) Andrásy, 1986 ^a	Rhabditida
Qudsianematidae	Cephalobidae
<i>Amblydorylaimus isokaryon</i> (Loof, 1975) Andrásy, 1998 ^a	<i>Chiloplacoides antarcticus</i> Heyns, 1994 ^a
<i>Eudorylaimus coniceps</i> Loof, 1975 ^a	<i>Scottnema lindsayae</i> Timm, 1971 ^a
<i>E. pseudocarteri</i> Loof, 1975 ^a	Panagrolaimidae
<i>E. spaulli</i> Loof, 1975 ^a	<i>Panagrolaimus davidi</i> Timm, 1971 ^a
<i>E. verrucosus</i> Loof, 1975 ^a	<i>P. magnivulvatus</i> Boström 1995 ^a
Enoplida	Rhabditidae
Alaimidae	<i>Dolichorhabditis tereticorpus</i> Kito and Ohyama, 2008 ^c
<i>Paramphidelus antarcticus</i> Tsalolikhin, 1981 ^a	Diplogasteria
Mononchida	Tylenchida
Mononchidae	Belonolaimidae
<i>Coomansus gerrachei</i> (de Man, 1904) Jairajpuri and Khan, 1977 ^a	<i>Tylenchorhynchus maximus</i> Allen, 1954 ^b
Secernentea	Hoplolaimidae
Rhabditia	<i>Rotylenchus capensis</i> van den Berg & Harris, 1996 ^a
Rhabditida	Pratylenchidae
Rhabditidae	<i>Apratylenchoides joenssoni</i> Ryss, Boström and Sohlenius, 2005 ^b
<i>Cuticularia firmata</i> Andrásy, 1998 ^a	<i>Pratylenchus andinus</i> Lordello, Zamith and Boock, 1961 ^b
<i>Rhabditis krylovi</i> Tsalolikhin, 1989 ^a	Tylenchidae
	<i>Aglenchus gricola</i> (de Man, 1884) Andrásy, 1954 ^b

Table 1 continued

Maritime Antarctica	Continental Antarctica
Diplogasteria	Tylenchulidae
Aphelenchida	<i>Paratylenchus nanus</i> Cobb, 1923 ^b
Aphelenchoididae	
<i>Aphelenchoides haguei</i> Maslen, 1979 ^a	
<i>A. helicosoma</i> Maslen, 1979 ^a	
<i>A. vaghani</i> Maslen, 1979 ^a	
Tylenchida	
Anguinidae	
<i>Ditylenchus parcevivens</i> Andr�ssy, 1998 ^a	
Tylenchidae	
<i>Antarctenchus hooperi</i> Spaul, 1972 ^a	
Total = 32	Total = 23

Superscript numbers indicate literature sources: ^a Andr ssy (1998), ^b Andr ssy and Gibson (2007), ^c Kito and Ohyama (2008)

competition and predation in some of the microhabitats in Dronning Maud Land (Sohlenius and Bostr m 2008). Because of the relatively high diversity of the maritime Antarctic nematode communities (i.e., Maslen and Convey 2006; Nielsen et al. 2011), biotic interactions are likely important drivers of community composition. However, because so few communities have been examined to date, inferences such as this are still premature. It has been shown, though, that vegetated sites in the maritime Antarctic (i.e., productive soils) generally support the highest nematode densities (B lter et al. 1997; Convey and Wynn-Williams 2002) and soil properties such as pH and soil moisture influence the community composition (Nielsen et al. 2011).

Though few in number, Antarctic nematode species are well adapted to their harsh environment (Turner et al. 2009). One survival strategy used by many Antarctic nematodes is anhydrobiosis (Treonis and Wall 2005), in which the organisms desiccate in order to survive extreme water limitation and low temperatures as well as other stresses (this is also found in tardigrades and rotifers; Crowe et al. 1992; Wharton and Barclay 1993; Wright et al. 1992). Moreover, the only known animal that can survive intracellular freezing is the Antarctic nematode *Panagrolaimus davidi* (Wharton and Ferns 1995). Additionally, gene expression in the nematode *Plectus murrayi* has been optimized to survive both desiccation and freezing (Adhikari et al. 2010), which is a testament to the considerable evolutionary adaptations for some of the Antarctic soil animals. Most species, however, are considered cold tolerant (psychrotrophic, i.e., maximal growth at higher temperatures) rather than cold adapted (or requiring; psychrophilic, i.e., grow optimally at low temperatures) per se, and it has been suggested that their physiological capabilities will allow them to cope with

increases in temperature and water availability (Block et al. 2009). However, responses of nematode growth rates and fecundity to temperature are species specific. For example, the nematode *P. davidi*, a microbivore associated with moss and algal patches in coastal regions of the Ross Sea region, shows the highest growth rates at temperatures between 25 and 30 C (Brown et al. 2004). Likewise, the microbivore *P. antarcticus* found in maritime Antarctica shows optimal growth rates and fecundity at or above 10 C (temperatures up to 22 C increased growth rates but had no further influence on fecundity; Caldwell 1981). In contrast, the growth rate of the microbivorous nematode *S. lindsayae*, which dominates the dry salty soils of the polar deserts in the MDVs, appears to be negatively affected by temperatures >10 C (Overhoff et al. 1993). Such differences will result in species-specific responses to climate change.

Observed and predicted climate changes

In recent years, rapid, albeit complex changes in local climate have been observed in Antarctica, particularly on the Antarctic Peninsula, with substantial impacts on marine and terrestrial ecosystems (Ducklow et al. 2007; Turner et al. 2009). For instance, the average annual surface temperature increased by 0.56 C per decade near the Faraday/Vernadsky Station over the last 5 decades of the twentieth century (mainly due to higher winter temperatures; Turner et al. 2005). At larger scales, significant, albeit smaller increases in surface temperature have also been observed. A recent study showed that the temperature in Antarctica increased by approximately 0.12 C per decade between 1957 and 2006, with the most pronounced change occurring over West Antarctica ($\sim 0.17^\circ\text{C dec}^{-1}$)

and a weaker change observed over East Antarctica ($\sim 0.10^{\circ}\text{C dec}^{-1}$; Steig et al. 2009). Yet, different trends have been observed at smaller spatial and temporal scales, and temperatures have been stable or even decreasing in some regions within continental Antarctica (Bertler et al. 2004; Thompson and Solomon 2002; Turner et al. 2005). For example, a notable decrease in temperature was observed in the MDVs between 1986 and 2000 (Doran et al. 2002). Moreover, significant changes in snowfall and moisture regimes related to long-term climate variation have been observed in East Antarctica (Hodgson et al. 2006).

Despite the observed idiosyncratic climate changes, a more directional warming and an increase in precipitation is expected to occur across Antarctica during the twenty-first century. A recent assessment of the models developed for the Intergovernmental Panel on Climate Change (IPCC) indicated that surface temperatures over the continent will increase by $0.34^{\circ}\text{C dec}^{-1}$ (or about 3°C in total) while precipitation will increase by $2.9 \text{ mm a}^{-1} \text{ dec}^{-1}$ (Bracegirdle et al. 2008). The expected temperature increases will be greatest over the continental high-altitude interior of East Antarctica and will be accompanied by a 20% increase in snowfall (Bracegirdle et al. 2008), of which most will fall during winter (Turner et al. 2009).

Another important aspect of the predicted climate changes is an increase in the frequency of extreme events (IPCC 2007). Accordingly, recent models have shown that the frequency of temperature extremes, i.e., heat waves (defined as $>5^{\circ}\text{C}$ above average daily temperature for at least 5 consecutive days), will increase (Tebaldi et al. 2006). Such events will lead to dramatic increases in moisture availability along the Antarctic coastline. Although these events are also predicted for interior Antarctica, the temperature increase during these heat waves is not large enough to lead to any significant melting and is therefore not likely to have a great impact on moisture availability (at least in the short term; Tebaldi et al. 2006). Similarly, Krinner et al. (2007) found that the frequency of extreme precipitation events (defined as days with >5 times the average daily precipitation) would increase near ice sheet domes and ridges with the greatest change in East Antarctica.

Nematode communities and climate change

In this section, we focus on the observed and predicted impacts of climate change on nematode communities in maritime and continental Antarctica with emphasis on temperature and precipitation changes. It should be noted that the inherent problem with such predictions are that the realized change in soil temperature and soil moisture levels

will depend strongly on local characteristics. For example, wet and vegetated soil are likely to show lower temperature variability over short time scales (i.e., hours) than dry or non-vegetated soils, and soils on north facing slopes will be warmer than soils on south facing slopes (Block et al. 2009; Turner et al. 2009). Soil moisture is in contrast more likely to be associated with the local topography and soil type, and temperature could negatively impact soil moisture levels through increased evaporation. However, for simplicity we make the assumption here that soils will, on average, become warmer and wetter with increasing temperatures and higher rates of precipitation.

Direct effects of climate change

A few studies have explored the relationship between nematode communities and climate change in Antarctica. However, among these there are several long-term observational studies that report significant relationships between nematodes (both at the species and at the community level) and local climate trends as well as extreme events, and a few that show impacts of climate manipulations.

The climate cooling observed in the MDVs between 1986 and 2000 (Doran et al. 2002) had a negative impact on the abundance of the dominant nematode *S. lindsayae* (Barrett et al. 2008a). Estimates suggest that the abundance of *S. lindsayae* decreased by about 65% between 1993 and 2005 throughout Taylor Valley (Barrett et al. 2008b). As this species dominates the food web in the majority of Taylor Valley soils, its sudden decrease in abundance had a significant impact on soil nutrient cycling. It was estimated that this caused a 32% reduction in soil carbon cycling (Barrett et al. 2008b). This cooling trend has been interrupted by infrequent warm years, with significant and long-lasting impacts on local communities. In particular, a warm summer in 2001–2002 produced a “pulse event” with high stream flow and local melting of permafrost creating seeps (Lyons et al. 2005; Wall 2007), resulting in increased soil moisture availability throughout Taylor Valley. The effect of increased water availability was recognizable for several years (Barrett et al. 2008a). For example, the nematode *Eudorylaimus* sp., which in the MDVs prefers more moist soils (Courtright et al. 2001), showed significant increases in abundance concomitant with the increased soil moisture availability that was observed between 2001 and 2005 (Barrett et al. 2008a).

The effects of high stream flow during the warm summer of 2001–2002 were also observed at one of the experimental sites used to simulate climate changes as outlined by Wall (2007) and Simmons et al. (2009). This experimental plot was flooded during the high-flow event, which saturated soils and decreased salinity, resulting in

changes to soil fauna community structure and composition. In particular, the densities of *S. lindsayae* decreased while the densities of *Eudorylaimus* sp. increased (Simmons et al. 2009), which corresponds with the predicted changes in habitat suitability (Courtright et al. 2001; Poage et al. 2008). A similar response to changes in habitat suitability was observed in a study where snow fences were employed to increase the size and duration of snow packs (Ayres et al. 2010) and in a study examining community change along moisture gradients caused by meting snow patches (Gooseff et al. 2003). The increased snow accumulation created by the snow fences led to greater soil moisture throughout the area subjected to snowcover, and the authors observed a subsequent decline in the abundance of *S. lindsayae* and an increase in *Eudorylaimus* sp. This pattern was only observed at one of the two experimental sites used in the study but it appeared at the site where changes in snow accumulation were most pronounced (Ayres et al. 2010). Similarly, soils under natural snow patches showed greater invertebrate abundance and diversity (Gooseff et al. 2003).

The negative response of *S. lindsayae* abundance to natural climate cooling within Taylor Valley contrasts with the findings of experimental climate manipulations in the same valley (Simmons et al. 2009). In this study, the authors subjected soils to warming using ITEX open-top chambers (e.g., the International Tundra Experiment; Marion et al. 1997) and water additions over 8 years and hypothesized that this would increase habitat suitability and therefore have a positive influence on soil nematode communities (i.e., higher abundances and more diverse communities). However, over the course of the experiment, *S. lindsayae* abundance decreased by 42% in the warming treatment while water additions had no influence on the nematode communities. The discrepancies between the responses to natural climate cooling and experimental warming (i.e., they both lead to decreased abundances despite the opposite climate trends) indicate the complexity of these systems but this may be explained by the nature of the dry, saline soils of the MDVs. Long-term monitoring of soil temperature and soil moisture at one of the field sites used in the climate manipulation study indicated that not only were the temperatures greater in the warming plots but the treatment also tended to increase soil moisture (Simmons et al. 2009). The authors note that increased soil moisture (which is probably attributed to snow collecting in the open-top chambers) in combination with elevated temperatures may lead to higher salinity in the upper soil layers through evapo-concentration (Lyons et al. 2005), which might have impaired nematode densities in the warming plots. This contrasts with the impact of the high-flow event, where the large volume of water flowing

through the site led to a dilution of salt concentrations in the soils and a positive population response by some soil fauna species (Wall 2007).

Studies of climate change impacts on nematode communities in ecosystems outside the MDVs are scarce. However, in one of the few studies conducted, UV-absorbing perspex cloches were used to ameliorate the microclimate (in particular temperature and UV radiation) of sandy soils in the Mars Oasis on Alexander Island in maritime Antarctica (Convey and Wynn-Williams 2002). Over the first year, there was a strong positive response of nematode abundance to climate amelioration, mainly driven by a large increase in the abundance of the microbivore *Plectus* sp., as well as a significant change in nematode community composition. Over the next few years, total nematode densities dropped, while diversity increased, reaching levels similar to those measured in adjacent vegetated soils, but remaining above those measured in non-vegetated soils. This pattern of succession was attributed to the development of bryophyte cover under the UV-absorbing perspex cloches rather than to the direct effects of the climate manipulations per se (Convey 2003b), as we discuss in the next section.

Another factor associated with the predicted climate changes that could be biologically relevant is the frequency of freeze–thaw cycles. It is likely that increasing temperatures will increase the frequency with which organisms freeze, thaw, and freeze again, and it has been suggested that the physiological stress associated with this process could have a strong negative impact on the survival rate and therefore biomass of plants, animals, and microorganisms (Turner et al. 2009). Unfortunately, to date no studies have investigated the direct impact of frequency of freeze–thaw cycles on Antarctic nematodes, and we can make no predictions on the impact of this. However, it seems likely that such processes will inhibit new colonizers, i.e., species that are not adapted to freeze–thaw cycles, whereas native Antarctic species may still prosper and expand their range sizes.

Several other climate change variables have been proposed to have a direct impact on nematode communities. Of these, the increased UV radiation associated with the development of the “ozone hole” over Antarctica is often mentioned to be of high concern due to the potential impact on biotic communities (Kennedy 1995; Weiler and Penhale 1994). Although the Montreal Protocol now regulates the release of ozone depleting compounds, the Antarctic ozone hole is expected to last at least until 2060 (McKenzie et al. 2007). UV radiation might have an indirect influence on the nematode communities by damaging photo pigments and thus affecting primary productivity (Kennedy 1995) and by reducing soil fungal growth (Hughes et al. 2003). However, the soil itself provides effective protection from

UV radiation, and we expect that it is unlikely that the increased UV radiation will have a strong direct impact on the subterranean nematodes. Other factors that may influence nematode communities include changes in cloud cover, wind speed, nutrient deposition, concentration of pollutants, etc. (e.g., Kennedy 1995; Wall 2007; Turner et al. 2009), but currently our knowledge is insufficient to make any predictions of the impact of these.

Indirect effects of climate change

The examples listed in the previous section highlight the observed and potential direct effects of climate change on Antarctic nematode communities. However, climate change is likely to have large indirect impacts on nematode communities as well, in particular through the development of plant communities on presently bare soils or a change in current composition of plant communities. A warmer and wetter climate is predicted to increase the area of vegetated soils and plant species diversity (although local responses may vary; Turner et al. 2009). Considering the established links between nematode communities and plant communities, it is necessary to understand climate change responses of plant communities in Antarctica before we can predict responses belowground (Wall 2007).

The response of vegetation to climate warming is already evident. Some regions within Antarctica have been subjected to significant climate warming since 1957, which is particularly pronounced in maritime Antarctica (Steig et al. 2009). Over the same time period, range expansion has been observed for both vascular plants and bryophytes. For example, in maritime Antarctica both *D. antarctica* and *C. quitensis* increased their range sizes significantly between the 1960s and 1990 (Fowbert and Smith 1994; Smith 1994), although this trend appears to have stabilized in certain areas, such as on Argentine Island (Parnikoza et al. 2009). The fast range expansion observed on Argentine Island between the 1960s and 1990 was coincidental with rapid warming in this area (Fowbert and Smith 1994; Smith 1994), and the subsequent stabilization appears to be related to a lack of a temperature increase since 1990 (Parnikoza et al. 2009). Not only will a warmer and wetter Antarctic climate contribute to range expansions of native species, it may also provide a more suitable soil habitat for the successful colonization of new plant and soil species from other regions as well as from local soil seed banks to germinate and establish viable populations. For example, the moss *Entosthodon subnudun* germinated from propagules in soils collected at the summit of Coulman Island, northern Victoria Land (Lewis Smith and Ochyra 2006). Hence, the predicted climate changes are likely to have a large impact on plant communities (Turner et al. 2009) and their associated soil communities.

The link between nematode communities and the vegetation is highlighted by the long-term effects of climate manipulations on Alexander Island in southern maritime Antarctica (Convey 2003b). As described earlier, the authors used perspex screens to simulate climate amelioration with short-term impacts on the nematode densities (Convey and Wynn-Williams 2002) followed by a longer-term decrease in densities and an increase in species diversity to levels similar to those in adjacent vegetated soils, which coincided with the development of a bryophyte cover (Convey 2003b). This suggests that the nematode community response was driven by the development of a plant community rather than by the climate manipulations per se, and plant community responses to climate change could therefore direct belowground community changes. The potential for vegetation type changes to influence nematode communities will however depend on the local plant species pool as highlighted by a similar climate manipulation study in Ares Oasis on the same island (Convey 2003b). This study showed the same increase in *Plectus* sp. densities but no long-term development of community complexity despite the development of a similar, albeit more sparse, bryophyte cover. It was hypothesized that the idiosyncratic response to climate manipulations was due to the study site in Ares Oasis being further away from stable vegetated areas and a lower overall biodiversity (Convey 2003b). Although our knowledge about specific responses of nematode communities to vegetation types is inadequate, it is likely that the range expansion and increased plant species diversity will provide a greater area of more favorable habitats for nematodes, and other soil organisms, and enhance soil food web complexity and rates of nutrient cycling.

Predicted responses of nematode communities to climate changes

We predict that the climate changes expected for Antarctica in this century, i.e., a warmer and wetter climate, are likely to lead to major changes in nematode communities and associated soil biota.

Firstly, nematode densities are expected to increase initially due to a more favorable soil climate and subsequently due to increases in the biomass, diversity, and productivity of terrestrial vegetation, including algae and bryophytes (Wall 2007). Climate warming is predicted to lower environmental stress, increase the duration of metabolic activity, increase growth rates and shorten life cycles, and through these combined influences, increase population sizes (Convey 2006; Turner et al. 2009). However, increasing temperatures may alter species composition and favor opportunistic nematode species (i.e., species such as *P. davidi* and *Plectus*) over cold-adapted

species, including *S. lindsayae*, the current dominant species in the MDVs. Moreover, negative population responses may also occur in locations brought on by increased frequency of freeze–thaw cycles and lower soil moisture availability caused by greater evaporation associated with higher temperatures.

Secondly, the relative abundances of species can be expected to shift as different species respond to changes in specific microhabitat requirements, which will consequently lead to altered habitat suitability and alterations in community composition (Wall and Virginia 1999; Court-right et al. 2001; Wall 2007). Shifts in community composition may be enhanced by extreme events, which can have a disproportionately large impact on the communities (Barrett et al. 2008a) and are likely to become more prevalent in the twenty-first century. The impact of such events may however be both positive and negative depending on climate legacies and current local conditions (Wall 2007). Moreover, the rate of community development will depend on the spatial isolation of the site (i.e., very isolated sites will receive few colonizers).

Thirdly, the Antarctic fauna, including nematodes, is generally expected to be able to cope with the direct effects of the predicted changes in mean annual temperature and precipitation rates (at least in the short term) as the current natural climatic variation (in terms of daily and annual extremes) is well beyond the changes predicted and the physiological abilities displayed by the Antarctic fauna (Block et al. 2009; Convey 2003a). Furthermore, the large climatic variation within Antarctica along both latitudinal and elevational gradients is likely to provide opportunities for local species to find suitable habitats during climate change. We therefore hypothesize that there is little to no imminent risk of large-scale extinction of native nematode species although changes in range sizes and local distributional patterns (including potential small-scale extinctions) are very likely to occur particularly in light of the predicted increase in extreme events.

Fourthly, a warmer and wetter climate with better developed plant communities and more opportunities for anthropogenic transport of propagules (with increased access by scientists and tourists) is predicted to increase colonization by novel species (Frenot et al. 2005; Turner et al. 2009; Wall 2007). Such recent colonization by new species has already been observed (Convey 2008b). Immigration of new species is likely to increase the overall diversity, but may have a negative impact on species locally.

Finally, all of these changes will influence local food web dynamics and nutrient cycling (Barrett et al. 2008b). Where the local diversity of nematodes increases, the number of trophic levels may also increase leading to increased biotic interactions (i.e., competition, predation,

etc.). This will be most pronounced in areas, such as the MDVs, where the current diversity and importance of biotic interactions are low (Hogg et al. 2006).

Summary

Although there have been few empirical studies on the effect of climate change on nematode communities in Antarctica, the predicted climate changes are likely to have a significant impact on Antarctic nematode communities. Primary among these changes are increased biodiversity, population densities, and soil food web complexity. We expect these changes will be heterogeneous across spatial scales, but emphasize the need for a more thorough exploration of climate change impacts on Antarctic nematode communities. In particular, more large-scale coordinated efforts to explore climate change impacts across climatic gradients throughout Antarctica would better inform our inferences (e.g., Wall et al., in press). This information would help predict the extent of climate change impacts on Antarctic biota and identify the most sensitive Antarctic terrestrial ecosystems for conservation. The polar regions are experiencing higher rates of warming than most other ecosystems; thus, increasing our understanding of the effects of climate change on Antarctica's biotic communities will improve our ability to predict climate change impacts in other ecosystem types.

Acknowledgments The US National Science Foundation (DEB 0344834, OPP 0423595 and ANT 0840979) supported this work. We also thank David Wharton and an anonymous referee for helpful comments on an earlier version of the manuscript.

Conflicts of interest The authors declare that they have no conflict of interest.

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