

# Chapter 13

## Climate Change and Microbial Populations

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**Abstract** By 2100, the mean air temperature at the Earth's surface is predicted to increase by 1.4 °C to 5.8 °C, with a disproportionate effect at high altitudes and latitudes. This chapter reviews the currently available information regarding the responses of key microbial parameters, including diversity, community composition, abundance and functions, to climate change in Antarctic soils. For microorganisms inhabiting Antarctic soils, some insight has been gained by comparing microbial communities across latitudinal gradients, or through short-term laboratory incubations and field studies. Rapid responses of mosses, nematodes, soil algae, cyanobacteria, fungi, and bacteria have been observed in some Antarctic soils. Despite these interesting findings, it is difficult to specifically predict the effects of warming on Antarctic soil microorganisms. One reason is the extreme heterogeneity of soil habitats in this region, as they vary from moist eutrophic ornithogenic soils to nutrient- and water-limited Dry Valley soils. Climate change might have rapid and direct effects on soil microbes that are not otherwise limited, but the release of other limitations (e.g., water, nutrients) could be more important in several environments.

### 13.1 Introduction

Antarctic environments are extraordinary in the harshness of their climates, which are far more severe than northern climates at similar latitudes (Convey 2001). Environmental conditions are considered unfavourable in terrestrial Antarctic environments, with low thermal capacity of the substratum, frequent freeze–thaw and wet–dry cycles, low and transient precipitation, reduced humidity, rapid

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drainage and limited organic nutrients (Wynn-Williams 1990; Convey 1996). Furthermore, only 0.33 % of the Antarctic continent is ice free for some or all of the year (Fox et al. 1994), with much of this area representing cold rock deserts and nunataks. The vegetation of these ice-free habitats is characterized by low coverage and low productivity, being mainly composed of mosses and lichens, with only two vascular plant species. Antarctic food webs are consequently relatively simple and are characterized by the absence of insect and mammalian herbivores, so that most of the energy and materials found within primary producers enter a detritus, rather than a grazing, trophic pathway (Davis 1981; Heal and Block 1987). According to Kennedy (1996), cold temperatures and low moisture availability are probably the main limiting factors, resulting in the depauperate status of Antarctic habitats. Although the Antarctic continent has been isolated from other land masses for over 25 million years by the strong geophysical barriers of the Southern Ocean and South Polar Air Vortex, there is evidence that viable propagules can be transported from South America and around Antarctica (Marshall 1996; Hughes et al. 2004). Thus, aerobiological isolation probably does not limit microbial colonization. Biotic interactions such as predation and competition are also thought to play only a minor role in limiting life (Kennedy 1995; Convey 1996; Wall and Virginia 1999). Consequently, any amelioration in ambient temperatures, water availability or nutrient availability is expected to encourage the development of trophic complexity in these habitats (Kennedy 1995).

By 2100, the mean air temperature at the Earth's surface is predicted to increase by 1.4–5.8 °C, with a disproportionate effect at high altitudes and latitudes (Solomon et al. 2007). Strong regional differences are expected, especially in Antarctica. Indeed, a net cooling of Eastern Antarctica between 1966 and 2000 (Doran et al. 2002) appears to have coincided with a dramatic warming of the Antarctic Peninsula between 1951 and 2000, with an increase of 0.56 °C per decade (Turner et al. 2002), which resulted in the Antarctic Peninsula warming more rapidly than most other regions on the planet (Steig et al. 2009). Temperature increases in ice-free areas are expected to increase the availability of liquid water (originating from glacial and permafrost melting), potentially resulting in remarkable changes in ecosystem development (Cowan and Tow 2004). For instance, warming trends have been coupled to expanding ranges for vascular plants across the Antarctic Peninsula (Fowbert and Smith 1994; Smith 1994; Frenot et al. 2005; Convey and Smith 2006). For microbes, it was hypothesized that the responses of Antarctic soils will be driven mainly by nutrient and/or water limitations (Wynn-Williams 1996; Treonis et al. 2002; Wasley et al. 2006), similar to what is observed in Arctic soils (Ruess et al. 1999; Rinnan et al. 2007). In contrast, experimental evidence from a range of environments (including arctic and alpine systems) has suggested a variety of direct effects of warming on soil microbial communities (Zogg et al. 1997; Ruess et al. 1999; Deslippe et al. 2005; Rinnan et al. 2007) or associated nutrient cycling processes (de Klein and van Logtestijn 1996; Maag and Vinther 1996; Castaldi 2000; Dobbie and Smith 2001; Barnard et al. 2005). For microorganisms inhabiting Antarctic soils, some insight has been gained by comparing microbial communities across an Antarctic latitudinal gradient, which has been used as a proxy for

predicting long-term climatic trends (Yergeau et al. 2007a, b, c, 2009), or through short-term laboratory incubations (Treonis et al. 2002; Bokhorst et al. 2007a; Newsham and Garstecki 2007; Yergeau and Kowalchuk 2008). The few field studies that have been reported to date have shown modest effects of warming on soil organic matter decomposition, as well as other soil processes and bacterial temperature sensitivity (Treonis et al. 2002; Bokhorst et al. 2007a; Rinnan et al. 2009). Rapid responses of mosses, nematodes, soil algae, cyanobacteria, fungi and bacteria have been observed in some Antarctic soils (Kennedy 1996; Wynn-Williams 1996; Convey and Wynn-Williams 2002; Dennis et al. 2012; Yergeau et al. 2012).

This book chapter reviews the relatively sparse information that is currently available regarding the responses of key microbial parameters, including diversity, community composition, abundance and functions, to climate change in Antarctic soils. Given the central role of microorganisms in Antarctic soil nutrient cycling, this knowledge is crucial for predicting the trajectory of Antarctic terrestrial environments in response to climate change. Antarctic terrestrial ecosystems represent excellent model systems for studying the effects of global warming on microorganisms: the relative simplicity of these environments facilitates the examination of microbial communities and activities without the confounding complexity of higher trophic levels (Smith 1996; Convey and Smith 2006). In the extreme Antarctic environment, small increments in temperature, nutrient or water availability have potentially greater biological impacts than changes on a similar scale in less extreme environments, simply because they represent relatively larger improvements to environmental conditions.

Climate change could affect Antarctic soil microorganisms in two ways: (1) directly, by increasing average temperature, decreasing the frequency of freeze–thaw cycles and increasing water availability and (2) indirectly, through changes in vegetation and soil nutrient cycling. Both direct and indirect effects of global warming could be different in the short term and in the long term. Integrating experimental and gradient studies may help to distinguish between the transient short-term effects of climate change and lasting longer-term effects (Kennedy 1996; Dunne et al. 2004).

## 13.2 Direct Influence on Microbes

### 13.2.1 Temperature

Bacterial processes are particularly sensitive to environmental conditions (Eriksson et al. 2001), yet bacteria are also highly adaptable to extreme and changing environments (Cavicchioli et al. 2000; Georlette et al. 2004; Thomas 2005). Many terrestrial Antarctic bacteria are believed to be cold tolerant as opposed to cold adapted (Line 1988; Wery et al. 2003; Aislabie et al. 2006). This may not be surprising as cold-tolerant organisms are better suited to survive the large and

frequent variation in temperatures occurring in Antarctica than true cold-adapted microorganisms (Cowan and Tow 2004). This also implies that the selection pressure for low optimal growth temperature is relatively low compared with other environmental constraints (Vincent 2000).

Microbial responses to temperature are typically nonlinear, and therefore, it has been suggested that changes in temperature and climatic variability may have disproportionate effects on microbial communities and the functions for which they are responsible (Scherm and van Bruggen 1994). Most climate change scenarios predict not only a general warming trend, but also an increased variability in weather conditions (Solomon et al. 2007). This includes alterations in precipitation and thawing patterns, which will lead to more variable soil conditions (Groffman et al. 2001). Thus, predicted changes in temperature variability may have more profound consequences than increases in average temperature for Antarctic soil microorganisms, given the greater stress imposed by frequent temperature fluctuations as compared to gradual changes in average temperature (Vishniac 1993).

In the Antarctic, freeze–thaw cycles (FTC) are a common feature, and changes in the frequency of such events could have substantial effects on soil microbial communities and associated nutrient cycling functions. The freezing and thawing of soil has been shown to damage or destroy some microbial cells, releasing nutrients that become available to surviving microbes, which then become highly active during periods of thaw (Skogland et al. 1988; Christensen and Tiedje 1990). Extra substrate and nutrients can also be released from the physical disruption of soil aggregates due to frost action (Christensen and Christensen 1991; Edwards and Cresser 1992), resulting in altered microniches (Skogland et al. 1988). The penetration and effect of freezing and subsequent thawing depend on the level of insulation provided by vegetation and snow cover (Edwards and Cresser 1992). FTCs are also believed to play an important role in nutrient cycling in the Antarctic because they induce changes in exudation patterns of cryptogams (members of a formerly recognized taxonomic group that included all seedless plants and plantlike organisms) (Tearle 1987; Melick and Seppelt 1992; Melick et al. 1994). It has been estimated that freeze–thaw events induce an annual release of >15 % of the total organic matter of Antarctic cryptogams to the soil microbiota (Tearle 1987), an input that is ten times greater than what is estimated to arise from the decomposition of dead subsurface vegetation materials (Davis 1986). Accordingly, the frequency of FTCs was identified as a potentially important driving factor for the structuring of microbes involved in the C-cycle in Antarctic soils (Yergeau et al. 2007b).

### ***13.2.2 Water***

Water is a major limiting factor in some Antarctic environments, and changes in climate might partly relieve this limitation. Water limitation generally increases with increasing latitude (Kennedy 1993). Climate change could help relieve water limitations at some sites by (1) increasing precipitation, (2) changing precipitation

patterns, with rain replacing snow, (3) increasing water availability through increased glacier and permafrost melting and (4) increasing the period of time when water is available (longer growing season).

### 13.3 Indirect Influence on Microbes

As mentioned above, most of the microorganisms in Antarctic soils are believed to be cold tolerant as opposed to cold adapted. Consequently, it has been hypothesized that the direct effects of increasing temperature on Antarctic soilborne microorganisms will be less important than indirect effects, such as changes in vegetation density and other associated soil biophysical properties (Vishniac 1993; Panikov 1999).

#### 13.3.1 Plants

It has been suggested that ongoing climatic changes are steering existing terrestrial communities of the maritime Antarctic towards a more Magellanic or Patagonian composition (Kennedy 1996). The rapid warming rate of this region (2.8 °C since 1950, Turner et al. 2002) combined with the presence of a propagule bank in soils (Kennedy 1996) might speed up this shift in community composition. In fact, regional warming in the past decades has already led to a massive increase in the distribution of native Antarctic vascular plants (Fowbert and Smith 1994) and, together with an increased human presence, has also led to the introduction of non-native vascular plants (Molina-Montenegro et al. 2012). A recent study suggested that one of the two native Antarctic vascular plants, *Deschampsia antarctica*, has the ability to successfully compete with both soil microbes and moss for proteinaceous N at an early stage of decomposition that could explain the increasing success of this vascular plant as the maritime Antarctic warms (Hill et al. 2011). In ice-free areas that are too cold to support significant plant growth, indirect effects of climate change could also be seen through shifts in other primary producers such as lichens and cyanobacteria.

In the absence of consumers from higher trophic levels, such as herbivores, the link between plant and microbes is thought to be more important in Antarctic soils than in other environments, since a larger portion of the plant remains is made available to microorganisms. In fact, Antarctic soil microbial communities are significantly different between sparsely and densely vegetated environments (Yergeau et al. 2007a, 2009, 2012) and between rhizosphere and bulk soil of vascular plants (Teixeira et al. 2013). Not only is plant presence an important factor in structuring microbial communities, but also plant identity is of major importance, as different plant species exude distinct organic compounds, selecting for unique microbial communities (Kowalchuk et al. 2010). Roberts and colleagues (2009)

recorded higher concentrations of nitrate, total dissolved nitrogen, DOC, DON and free amino acids in soil under *D. antarctica* and *Colobanthus quitensis* than in lichen- or moss-dominated soils. As the majority of Antarctic plants are low rising and densely cover the ground below them, the presence of plants also provides a sort of physical sheltering to soil microbes. This physical sheltering means that water and temperature conditions are less variable under dense plant cover when compared with environments lacking this cover.

### ***13.3.2 Birds***

Climate warming and associated sea ice reduction in Antarctica have modified habitat conditions for certain Antarctic bird species including penguins, and these birds now demonstrate remarkable population responses to regional warming (Forcada et al. 2006). In the maritime Antarctic, densely vegetated sites covered by lichens, mosses and vascular plants are often linked to bird activity (Simas et al. 2008) and these soils are hot spots of microbial activity. Organic matter rich in carbon, nitrogen and phosphorus is added to the soil in the form of guano, feathers, eggshells and bird remains, which leads to the formation of ornithogenic soils (Aislabie et al. 2009) (Chap. 6). These soils can occur at active or abandoned penguin colonies, but also nearby rookeries of other large birds (e.g. skuas, petrels). Not only do birds change soil conditions for microbial life, but they also continuously inoculate soil with microorganisms through guano deposition. Recent work has indicated that the effect of birds on soil microbial communities varies with the extent and the type of ornithogenic input and, in highly ornithogenic soils, seems to be modulated by the species of bird present, due to differences in diet (Teixeira et al. 2013). The authors hypothesized that climate change will not only directly influence Antarctic soil microbial communities, but also indirectly influence them through shifts in bird populations (Teixeira et al. 2013).

### ***13.3.3 Other Soil Organisms***

Other soil organisms may also influence microbes in their response to climate change. For instance, some soil fauna (e.g. nematodes, protozoa) prey on bacteria and shifts in the populations of these species following climate change will influence bacterial populations. Antarctic nematodes have been shown to prefer certain microbial prey species (Newsham et al. 2004), which could induce indirect shifts in microbial community composition following climate change.

## 13.4 Observed Microbial Shifts

This section focuses on the shifts observed in microbial communities following experimental climate change in the field or in the laboratory. The variability between habitats and even within habitats makes it particularly difficult to generalize any of the trends observed.

### 13.4.1 Field Experimental Manipulation

The logistics of establishing and maintaining long-term field experiments in the Antarctic are very challenging, and up to now, very few studies were conducted. In one instance, microbial crusts consisting predominantly of filamentous cyanobacteria covered 74 % of the soil after 3 years of warming compared to only 5 % coverage for controls (Wynn-Williams 1993). However, comparison of colonization between different sites showed that water limitations may outweigh the effects of temperature (Wynn-Williams 1996). Wynn-Williams (1996) also reported that the nature and extent of warming responses in frost-sorted polygon soils depended on the composition of the initial microflora. For instance, N<sub>2</sub>-fixing cyanobacteria had a selective advantage specifically in N-limited fell-field (Wynn-Williams 1996).

Another study established warmed plots using open-top chambers (OTCs) at three different locations spread across 1,900 km in the Antarctic and sub-Antarctic. At each of these locations, densely vegetated and scarcely vegetated plots were established. Following two years of manipulation, very limited effects were observed on vegetation, arthropods, soil respiration and decomposition (Bokhorst et al. 2007a, b, 2008). Decomposition was more strongly influenced by local substratum characteristics (especially soil N availability) and plant functional type composition than by large-scale temperature differences (Bokhorst et al. 2007a). However, after three years of manipulation, differences did emerge, with an average of 33 % higher soil respiration in warmed plots (Yergeau et al. 2012). This increase in respiration was linked to a consistent increase in the abundance of fungi across all plots and an increase in bacterial abundance in densely vegetated plots (Yergeau et al. 2012). Consistent shifts across all environments were also observed in bacterial community composition, with a decrease in *Acidobacteria* and an increase in *Alphaproteobacteria* with warming (Yergeau et al. 2012). These shifts could also be linked to increased respiration as *Acidobacteria* generally display an oligotrophic lifestyle (slow growers) and *Alphaproteobacteria* are generally thought of as copiotrophs (fast growers) (Yergeau et al. 2012). Following warming, there was also a decrease in the functional redundancy of microorganisms, with fewer variants of several key functional genes being detected (Yergeau et al. 2012). All these results suggest increased nutrient availability following warming, but this trend remains to be confirmed over longer time scales. In contrast, three years of warming did not significantly alter bacterial temperature adaptation or

growth rate (measured by leucine incorporation) with an overwhelming effect of location and vegetation on this parameter (Rinnan et al. 2009).

Another recent study subjected soils to OTC warming and nutrient addition at one northern maritime (Wynn Knolls, Signy Island) and one southern maritime Antarctic location (Mars Oasis) (Dennis et al. 2012). Responses to the warming treatment were not detected at Wynn Knolls, where OTCs increased mean monthly soil temperatures by up to 0.7 °C. At Mars Oasis, however, where OTCs increased monthly soil temperatures by up to 2.4 °C, warming led to 41 and 46 % reductions in the concentrations of Gram-positive bacterial markers in soil to which glycine and tryptic soy broth (TSB) had been applied, respectively, leading to a decrease of 55 and 51 % in the ratio of Gram-positive to Gram-negative markers in these soils (Dennis et al. 2012). These data suggest that warming may constrain the responses of bacterial communities to carbon and nitrogen inputs arising from dead plant matter entering maritime Antarctic soils in future decades (Dennis et al. 2012).

In the Dry Valleys, no significant effect of warming and wetting on cotton strip decomposition was observed in field manipulations (Treonis et al. 2002). In contrast to moist maritime Antarctic soils, soil processes in the Dry Valleys appeared to mainly be limited by the very low moisture content and this limitation constrains any response to improving environmental conditions (Treonis et al. 2002).

In contrast to some Antarctic soils, bacterial biomass in Arctic soils was reported to be virtually unaffected by artificially increased temperature (Jonasson et al. 1999; Ruess et al. 1999; Schmidt et al. 2002). However, a recent study pointed out that bacteria indeed responded to increased temperature, but that more than a decade of increased temperature was necessary to detect changes in bacterial communities, and that likely even more would be required to elicit a response from fungal communities (Rinnan et al. 2007). It thus appears that some Antarctic environments may respond more rapidly than Arctic environments and that the difference in response time might be related to the relative trophic simplicity of Antarctic environments. Another source of disparity between northern and southern polar regions is that Antarctic climates are far more severe than northern climates at similar latitudes (Convey 2001). Antarctic terrestrial environments also have a much greater degree of physical isolation.

### ***13.4.2 Laboratory Experimental Manipulation***

Several studies included both field manipulations and laboratory incubation of soils. In most cases, the laboratory experiment induced larger changes in microbial communities since the magnitude of the change imposed was larger. For instance, Dry Valleys soils did not respond to field manipulation, but laboratory incubation of microcosms, in which soil moisture was increased to 10 % (as compared to 0.6 %), led to increased soil respiration, nitrification and cotton strip decomposition (Treonis et al. 2002). Similarly, an increase of 4 or 8 °C in laboratory incubation led to higher organic matter breakdown, as compared to a lack of response

during field warming (where experimental temperatures were increased by  $<1$  °C) (Bokhorst et al. 2007a). These studies suggest that substantial changes are required before significant effects can be detected, and these are often well above the magnitude of the change that is expected to occur in reality.

Global warming will not only raise average temperatures, but also decrease the frequency of freeze–thaw cycles (FTC) at several Antarctic locations. Yergeau and Kowalchuk (2008) sought to contrast the effects of temperature and FTC by using two sets of microcosm experiments. Results showed that bacteria were more affected by warming than by changes in FTC frequency, while fungal community structure and abundance was mostly influenced by FTC frequency and the presence of vegetation (Yergeau and Kowalchuk 2008). The relative densities of several bacterial gene families involved in key steps of the N-cycle were affected by FTCs, while warming had little or no effect (Yergeau and Kowalchuk 2008). FTCs and incubation temperature also significantly influenced laccase enzymatic activity in soil (Yergeau and Kowalchuk 2008).

An interesting study looked at the interactive effects of bacterial predator flagellate species loss and temperature on the abundance of bacteria and the concentration of ammonium in the growth media (Newsham and Garstecki 2007). After 252 h, bacterial abundance was reduced by 75 % and  $\text{NH}_4$  concentrations doubled in mixtures inoculated with six and four flagellate species, compared with those inoculated with two species, but only in warmed microcosms. This difference in response was apparently largely owing to the absence of *Bodo saltans* and *Spumella putida*, species with high grazing activities and growth rates, from most replicates of the warmed two species mixtures. The authors concluded that random species loss from food webs or communities is likely to alter the responses of bacteria to environmental change, largely owing to interspecific differences in responses to change (Newsham and Garstecki 2007).

## 13.5 Conclusions

In summary, despite the interesting findings of previous studies, it is difficult to specifically predict the effects of warming on Antarctic soil microorganisms. One reason is the extreme heterogeneity of soil habitats in this region, as they vary from moist eutrophic ornithogenic soils to nutrient- and water-limited Dry Valley soils. Climate change might have rapid and direct effects on soil microbes that are not otherwise limited, but the release of other limitations (e.g. water, nutrients) could be more important in several environments. In these environments, the indirect effects of climate change through the modulation of plant and bird communities are likely to be more important than the direct effects of climate change for microbial communities. Some interesting approaches could be useful to further increase the knowledge that was presented in this chapter: (1) a longer-term field experiment with factorial manipulation of temperature, nitrogen and water at various locations would help disentangling the relative effects of nutrient and

water limitations versus warming; (2) monitoring soil microbial communities in a range of Antarctic environments for a long period of time would be helpful in revealing shifts in natural microbial communities due to ongoing global warming, analogous to what has been done for vascular plant communities (Fowbert and Smith 1994; Smith 1994; Convey 2003); (3) increase the use of high-resolution state-of-the-art molecular methods such as metatranscriptomics and metagenomics which may reveal subtle changes in microbial communities that would otherwise be undetectable. However, following the evidence presented in this chapter, it can already be said quite confidently that in the long run, global warming will have profound effects on Antarctic soil microorganisms.

## References

- Aislabie JM, Chhour KL, Saul DJ, Miyauchi S, Ayton J, Paetzold RF, Balks MR (2006) Dominant bacteria in soils of Marble Point and Wright Valley, Victoria Land, Antarctica. *Soil Biol Biochem* 38:3041–3056
- Aislabie J, Jordan S, Ayton J, Klassen JL, Barker GM, Turner S (2009) Bacterial diversity associated with ornithogenic soil of the Ross Sea region, Antarctica. *Can J Microbiol* 55:21–36
- Barnard R, Leadley PW, Hungate BA (2005) Global change, nitrification, and denitrification: a review. *Glob Biogeochem Cy* 19:1007
- Bokhorst S, Huiskes AHL, Convey P, Aerts R (2007a) Climate change effects on organic matter decomposition rates in ecosystems from the Maritime Antarctic and Falkland Islands. *Glob Change Biol* 13:2642–2653
- Bokhorst S, Huiskes AHL, Convey P, Aerts R (2007b) The effect of environmental change on vascular plant and cryptogam communities from the Falkland Islands and the Maritime Antarctic. *BMC Ecol* 7:15
- Bokhorst S, Huiskes AHL, Convey P, van Bodegom PM, Aerts R (2008) Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. *Soil Biol Biochem* 40:1547–1556
- Castaldi S (2000) Responses of nitrous oxide, dinitrogen and carbon dioxide production and oxygen consumption to temperature in forest and agricultural light-textured soils determined by model experiment. *Biol Fertil Soils* 32:67–72
- Cavicchioli R, Thomas T, Curmi PMG (2000) Cold stress response in Archaea. *Extremophiles* 4:321–331
- Christensen S, Christensen BT (1991) Organic matter available for denitrification in different soil fractions: effect of freeze/thaw cycles and straw disposal. *J Soil Sci* 42:637–647
- Christensen S, Tiedje JM (1990) Brief and vigorous N<sub>2</sub>O production by soil at spring thaw. *J Soil Sci* 41:1–4
- Convey P (1996) The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. *Biol Rev* 71:191–225
- Convey P (2001) Antarctic ecosystems. *Encyclopedia Biodiversity* Acad Press San Diego, pp 171–184
- Convey P (2003) Maritime Antarctic climate change: signals from terrestrial biology. *Antarct Res Ser* 79:145–158
- Convey P, Smith RIL (2006) Responses of terrestrial Antarctic ecosystems to climate change. *Plant Ecol* 182:1–10
- Convey P, Wynn-Williams DD (2002) Antarctic soil nematode response to artificial climate amelioration. *Eur J Soil Biol* 38:255–259

- Cowan DA, Tow LA (2004) Endangered Antarctic environments. *Annu Rev Microbiol* 58:649–690
- Davis RC (1981) Structure and function of two Antarctic terrestrial moss communities. *Ecol Monogr* 51:125–143
- Davis RC (1986) Environmental-factors influencing decomposition rates in two Antarctic moss communities. *Polar Biol* 5:95–103
- de Klein CAM, van Logtestijn RSP (1996) Denitrification in grassland soils in The Netherlands in relation to irrigation, N-application rate, soil water content and soil temperature. *Soil Biol Biochem* 28:231–237
- Dennis PG, Newsham KK, Rushton SP, Ord VJ, O'Donnell AG, Hopkins DW (2012) Warming constrains bacterial community responses to nutrient inputs in a southern, but not northern, maritime Antarctic soil. *Soil Biol Biochem* 57:248–255
- Deslippe JR, Egger KN, Henry GHR (2005) Impacts of warming and fertilization on nitrogen-fixing microbial communities in the Canadian High Arctic. *FEMS Microbiol Ecol* 53:41–50
- Dobbie KE, Smith KA (2001) The effects of temperature, water-filled pore space and land use on N<sub>2</sub>O emissions from an imperfectly drained gleysol. *Eur J Soil Sci* 52:667–673
- Doran PT, Priscu JC, Lyons WB, Walsh JE, Fountain AG, McKnight DM, Moorhead DL, Virginia RA, Wall DH, Clow GD, Fritsen CH, McKay CP, Parsons AN (2002) Antarctic climate cooling and terrestrial ecosystem response. *Nat* 415:517–520
- Dunne JA, Saleska SR, Fischer ML, Harte J (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology* 85:904–916
- Edwards AC, Cresser MS (1992) Freezing and its effects on chemical and biological properties of soil. *Adv Soil Sci* 18:59–79
- Eriksson M, Ka JO, Mohn WW (2001) Effects of low temperature and freeze-thaw cycles on hydrocarbon biodegradation in Arctic tundra soil. *Appl Environ Microbiol* 67:5107–5112
- Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biol* 12:411–423
- Fowbert JA, Smith RIL (1994) Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. *Arct Alp Res* 26:290–296
- Fox AJ, Paul A, Cooper R (1994) Measured properties of the Antarctic ice sheet derived from the SCAR Antarctic digital database. *Polar Rec* 30:201–206
- Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M, Bergstrom DM (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biol Rev* 80:45–72
- Georlette D, Blaise V, Collins T, D'Amico S, Gratia E, Hoyoux A, Marx JC, Sonan G, Feller G, Gerday C (2004) Some like it cold: biocatalysis at low temperatures. *FEMS Microbiol Rev* 28:25–42
- Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzbugh RD, Tierney GL (2001) Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochem* 56:135–150
- Heal OW, Block W (1987) Soil biological processes in the North and South. *Ecol Bull* 38:47–57
- Hill PW, Farrar J, Roberts P, Farrell M, Grant H, Newsham KK, Hopkins DW, Bardgett RD, Jones DL (2011) Vascular plant success in a warming Antarctic may be due to efficient nitrogen acquisition. *Nat Clim Change* 1:50–53
- Hughes KA, McCartney HA, Lachlan-Cope TA, Pearce DA (2004) A preliminary study of airborne microbial biodiversity over peninsular Antarctica. *Cell Mol Biol* 50:537–542
- Jonasson S, Michelsen A, Schmidt IK, Nielsen EV (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. *Ecology* 80:1828–1843
- Kennedy AD (1993) Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. *Arct Alp Res* 25:308–315
- Kennedy AD (1995) Antarctic terrestrial ecosystem response to global environmental-change. *Annu Rev Ecol Syst* 26:683–704
- Kennedy AD (1996) Antarctic fellfield response to climate change: a tripartite synthesis of experimental data. *Oecologia* 107:141–150

- Kowalchuk GA, Yergeau E, Leveau JHJ, Sessitch A, Bailey M (2010) Plant-associated microbial communities. *Environ Mol Microbiol*, pp 133–147
- Line MA (1988) Microbial-flora of some soils of Mawson Base and the Vestfold Hills, Antarctica. *Polar Biol* 8:421–427
- Maag M, Vinther FP (1996) Nitrous oxide emission by nitrification and denitrification in different soil types and at different soil moisture contents and temperatures. *Appl Soil Ecol* 4:5–14
- Marshall WA (1996) Biological particles over Antarctica. *Nature* 383:680
- Melick DR, Seppelt RD (1992) Loss of soluble carbohydrates and changes in freezing-point of Antarctic bryophytes after leaching and repeated freeze–thaw cycles. *Antarct Sci* 4:399–404
- Melick DR, Bolter M, Moller R (1994) Rates of soluble carbohydrate utilization in soils from the Windmill Islands Oasis, Wilkes Land, continental Antarctica. *Polar Biol* 14:59–64
- Molina-Montenegro MA, Carrasco-Urra F, Rodrigo C, Convey P, Valladares F, Gianoli E (2012) Occurrence of the non-native annual bluegrass on the Antarctic mainland and its negative effects on native plants. *Conserv Biol* 26:717–723
- Newsham KK, Garstecki T (2007) Interactive effects of warming and species loss on model Antarctic microbial food webs. *Funct Ecol* 21:577–584
- Newsham KK, Rolf J, Pearce DA, Strachan RJ (2004) Differing preferences of Antarctic soil nematodes for microbial prey. *Eur J Soil Biol* 40:1–8
- Panikov NS (1999) Understanding and prediction of soil microbial community dynamics under global change. *Appl Soil Ecol* 11:161–176
- Rinnan R, Michelsen A, Bååth E, Jonasson S (2007) Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. *Glob Change Biol* 13:28–39
- Rinnan R, Rousk J, Yergeau E, Kowalchuk GA, Bååth E (2009) Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: predicting responses to climate warming. *Glob Change Biol* 15:2615–2625
- Roberts P, Newsham KK, Bardgett RD, Farrar JF, Jones DL (2009) Vegetation cover regulates the quantity, quality and temporal dynamics of dissolved organic carbon and nitrogen in Antarctic soils. *Polar Biol* 32:999–1008
- Ruess L, Michelsen A, Schmidt IK, Jonasson S (1999) Simulated climate change affecting microorganisms, nematode density and biodiversity in subarctic soils. *Plant Soil* 212:63–73
- Scherm H, van Bruggen AHC (1994) Global warming and nonlinear growth: how important are changes in average temperature? *Phytopathology* 84:1380–1384
- Schmidt IK, Jonasson S, Shaver GR, Michelsen A, Nordin A (2002) Mineralization and distribution of nutrients in plants and microbes in four Arctic ecosystems: responses to warming. *Plant Soil* 242:93–106
- Simas FNB, Schaefer CEGR, Filho MRA, Francelino MR, Filho EIF, da Costa LM (2008) Genesis, properties and classification of Cryosols from Admiralty Bay, maritime Antarctica. *Geoderma* 144:116–122
- Skogland T, Lomeland S, Goksoyr J (1988) Respiratory burst after freezing and thawing of soil: experiments with soil bacteria. *Soil Biol Biochem* 20:851–856
- Smith RIL (1994) Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia* 99:322–328
- Smith RIL (1996) Terrestrial and freshwater biotic components of the western Antarctic peninsula. *Antarct Res Ser* 70:15–59
- Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (2007) Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. *Clim Change* 2007: Physical Sci Basis 996
- Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC, Shindell DT (2009) Warming of the Antarctic ice-sheet surface since the 1957 International Geophysical Year. *Nature* 457:459–462
- Tearle PV (1987) Cryptogamic carbohydrate release and microbial response during freeze-thaw cycles in Antarctic fellfield fines. *Soil Biol Biochem* 19:381–390

- Teixeira LCRS, Yergeau E, Balieiro FC, Piccolo MC, Peixoto RS, Rosado AS, Greer CW (2013) Plant and bird presence strongly influences the microbial communities in soils of Admiralty Bay, Maritime Antarctica. *PLoS One* 8(6):e66109
- Thomas DN (2005) Photosynthetic microbes in freezing deserts. *Trends Microbiol* 13:87–88
- Treonis AM, Wall DH, Virginia RA (2002) Field and microcosm studies of decomposition and soil biota in a cold desert soil. *Ecosystem* 5:159–170
- Turner J, King JC, Lachlan-Cope TA, Jones PD (2002) Recent temperature trends in the Antarctic. *Nature* 418:291–292
- Vincent WF (2000) Evolutionary origins of Antarctic microbiota: invasion, selection and endemism. *Antarct Sci* 12:374–385
- Vishniac HS (1993) The microbiology of Antarctic soils. *Antarct Microbiol* 297–341
- Wall DH, Virginia RA (1999) Controls on soil biodiversity: insights from extreme environments. *Appl Soil Ecol* 13:137–150
- Wasley J, Robinson SA, Lovelock CE, Popp M (2006) Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water. *Global Change Biol* 12:1800–1812
- Wery N, Gerike U, Sharman A, Chaudhuri JB, Hough DW, Danson MJ (2003) Use of a packed-column bioreactor for isolation of diverse protease-producing bacteria from antarctic soil. *Appl Environ Microbiol* 69:1457–1464
- Wynn-Williams DD (1990) Ecological aspects of Antarctic microbiology. *Adv Microb Ecol* 11:71–146
- Wynn-Williams DD (1993) Microbial processes and initial stabilization of fell-field soil. *Primary Succession Land*, pp 17–32
- Wynn-Williams DD (1996) Response of pioneer soil microalgal colonists to environmental change in Antarctica. *Microb Ecol* 31:177–188
- Yergeau E, Kowalchuk GA (2008) Responses of Antarctic soil microbial communities and associated functions to temperature and freeze-thaw cycle frequency. *Environ Microbiol* 10:2223–2235
- Yergeau E, Bokhorst S, Huiskes AHL, Boschker HTS, Aerts R, Kowalchuk GA (2007a) Size and structure of bacterial, fungal and nematode communities along an Antarctic environmental gradient. *FEMS Microbiol Ecol* 59:436–451
- Yergeau E, Kang S, He Z, Zhou J, Kowalchuk GA (2007b) Functional microarray analysis of nitrogen and carbon cycling genes across an Antarctic latitudinal transect. *ISME J* 1:163–179
- Yergeau E, Newsham KK, Pearce DA, Kowalchuk GA (2007c) Patterns of bacterial diversity across a range of Antarctic terrestrial habitats. *Environ Microbiol* 9:2670–2682
- Yergeau E, Schoondermark-Stolk SA, Brodie EL, Déjean S, DeSantis TZ, Gonçalves O, Piceno YM, Andersen GL, Kowalchuk GA (2009) Environmental microarray analyses of Antarctic soil microbial communities. *ISME J* 3:340–351
- Yergeau E, Bokhorst S, Kang S, Zhou JZ, Greer CW, Aerts R et al (2012) Shifts in soil microorganisms in response to warming are consistent across a range of Antarctic environments. *ISME J* 6:692–702
- Zogg GP, Zak DR, Ringelberg DB, MacDonald NW, Pregitzer KS, White DC (1997) Compositional and functional shifts in microbial communities due to soil warming. *Soil Sci Soc Am J* 61:475–481