

Experimentally increased snow accumulation alters soil moisture and animal community structure in a polar desert

Edward Ayres · Johnson N. Nkem · Diana H. Wall ·
Byron J. Adams · J. E. Barrett · Breana L. Simmons ·
Ross A. Virginia · Andrew G. Fountain

Received: 7 October 2009 / Revised: 20 December 2009 / Accepted: 17 January 2010 / Published online: 17 February 2010
© Springer-Verlag 2010

Abstract Snow accumulation can influence soil properties in arctic and alpine tundra, boreal and temperate forests, and temperate grasslands. However, snow may be even more influential in arid ecosystems, which by definition are water limited, such as the hyper-arid polar desert of the McMurdo Dry Valleys, Antarctica. Moreover, snow accumulation may be altered by climate change in the future. In order to investigate the impact of changes in snow accumulation on soils in the McMurdo Dry Valleys we experimentally manipulated the quantity of snow at two locations and monitored soil properties over 5 years in relation to a snow depth gradient created by snow fences. We predicted that increased snow depth would be associated with increased soil moisture and a shift in soil animal community structure. While we did not observe changes in soil

biochemistry or community structure along the snow depth gradient at either site, increased snow accumulation caused by the snow fence altered soil properties across the entire length of the transects at one site (Fryxell), which collected substantially more snow than the other site. At Fryxell, the presence of the snow fence increased gravimetric soil moisture from 1 to 5–9%. This was associated with a decline in abundance of the dominant animal, *Scottinema lindsayae*, a nematode typically found in dry soil, and an increase in *Eudorylaimus* sp. a nematode associated with moist soil. We also observed changes in soil pH, salinity, and concentrations of inorganic nitrogen and chlorophyll *a* over the course of the experiment, but it was difficult to determine if these were caused by snow accumulation or simply represented temporal variation related to other factors.

E. Ayres (✉) · J. N. Nkem · D. H. Wall · B. L. Simmons
Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins, CO 80523, USA
e-mail: eayres@neoninc.org

E. Ayres
Institute of Arctic and Alpine Research,
University of Colorado, Boulder, CO 80309-0450, USA

Present Address:

E. Ayres
National Ecological Observatory Network,
5340 Airport Blvd, Boulder, CO 80301, USA

Present Address:

J. N. Nkem
Center for International Forestry Research,
P.O. Box 6596 JKPWB, Jakarta 10065, Indonesia

D. H. Wall
Department of Biology, Colorado State University,
Fort Collins, CO 80523, USA

B. J. Adams
Department of Biology and Evolutionary Ecology Laboratories,
Brigham Young University, Provo, UT 84602, USA

J. E. Barrett
Department of Biological Sciences,
Virginia Tech, Blacksburg, VA 24061, USA

Present Address:

B. L. Simmons
Division of Natural Sciences and Mathematics,
East Georgia College, Swainsboro, GA 30401-2699, USA

R. A. Virginia
Environmental Studies Program,
Dartmouth College, Hanover, NH 03755, USA

A. G. Fountain
Department of Geology, Portland State University,
P.O. Box 751, Portland, OR 97207, USA

Keywords Snow fence · Soil biogeochemistry · Soil fauna · Precipitation change · Global change · Nematodes

Introduction

Snowfall and snowpack depth are increasingly recognized as important drivers of ecosystem structure and function in temperate, high latitude, and high-elevation terrestrial ecosystems (Walker et al. 1999; Groffman et al. 2001, 2006; Schimel et al. 2004; Barnett et al. 2005; Grippa et al. 2005; Kaste et al. 2008). Moreover, climate change is altering patterns of snowfall, as well as the depth, duration and water content of the snowpack, which in turn may alter ecosystem structure and function (Barnett et al. 2005; Mote et al. 2005; IPCC 2007). Increased snow depth insulates soil, which keeps soil temperatures warmer during winter than nearby areas with less snow accumulation (Walker et al. 1999; Groffman et al. 2001; Schimel et al. 2004; Kaste et al. 2008). In addition, snow melt provides significant amounts of moisture to many ecosystems, with areas that accumulate snow receiving greater amounts of moisture (Barnett et al. 2005). While the insulating properties of snow may have implications for most temperate, high latitude, and high-elevation terrestrial ecosystems that experience cold temperatures, the hydrological impacts of snow may be most pronounced in cold desert ecosystems, including parts of Antarctica, the Arctic, and the Gobi, which are by definition water limited.

The McMurdo Dry Valleys, the largest area of ice-free land in Antarctica, are cold and hyper-arid, with precipitation entirely in the form of snow. Snow accumulation in the valley bottom is low, typically ranging from 10 to 50 mm water equivalent (Fountain et al. 2009). Precipitation events in the dry valleys may cover the landscape with snow up to several centimeters deep, but much of this water is unavailable to soil organisms because of high sublimation rates (Chinn 1993; Treonis et al. 2000). Snow accumulations may persist for hours to days (summer) or a week to months (winter), depending on location in the valleys, and snow losses result primarily from wind erosion and sublimation (Chinn 1993; Campbell 2003; Fountain et al. 2009). The fraction of snow that melts is unknown but may be small (Campbell 2003; Gooseff et al. 2003). As a result, snow may influence local water availability largely through vapor diffusion into the soil. Wind is important in the re-distribution of snow in this ecosystem, as evidenced by the build up of snow on the leeward side of obstacles and relatively large deposition events during katabatic storms (Nylen et al. 2004; Fountain et al. 2009). These snow patches can be up to 1 m deep, cover tens of square meters in area, and are a significant source of moisture to nearby soil communities (Gooseff et al. 2003).

The harsh climatic conditions and poorly developed soils in the McMurdo Dry Valleys constrain biological diversity and activity. The soil is typically coarse (~95% sand) with extremely low levels of organic matter (<0.5% organic C), low moisture content (<2%), and high salinity (Campbell and Claridge 1987; Barrett et al. 2004; Ugolini and Bockheim 2008). Mosses and algae are the only form of vegetation in the Dry Valleys (Schwarz et al. 1992; Moorhead et al. 2003; Adams et al. 2006; Cannone et al. 2008), while five taxa of animals are found in the ecosystem: nematodes, tardigrades, rotifers, mites, and collembolans (Freckman and Virginia 1997; Stevens and Hogg 2002; Adams et al. 2006). The nematode *Scottinema lindsayae* is the most abundant and widely distributed animal in this ecosystem; other relatively common nematode species include *Eudorylaimus* sp. and *Plectus murrayi* (Freckman and Virginia 1997; Andrassy 1998, 2008; Adams et al. 2006). A survey of faunal occurrences in the Dry Valleys revealed that 35% of soils contained no animals, while ~50% contained nematodes only, and communities containing rotifer or tardigrades alone, together, or with nematodes accounted for the remaining ~15% of soils (Freckman and Virginia 1998).

The availability of water is a fundamental determinant of ecosystem structure and function in the McMurdo Dry Valleys, although other factors such as soil salinity and organic matter concentration are also important (Schwarz et al. 1992; Kennedy 1993; Freckman and Virginia 1997; Barrett et al. 2004; Poage et al. 2008). For example, mosses and algae are typically restricted to moist areas near lakes and ephemeral streams (Schwarz et al. 1992; Moorhead et al. 2003). The composition and complexity of the microbial food web varies with soil moisture (Connell et al. 2006; Fell et al. 2006; Barrett et al. 2008b), and transects from dry soil to lake or stream sediments mark major changes in biogeochemistry, concentrations of organic matter, and the abundance and community structure of animals (Treonis et al. 1999; Barrett et al. 2002; Moorhead et al. 2003; Elberling et al. 2006; Ayres et al. 2007).

Taylor Valley, the primary research site of the US McMurdo Long Term Ecological Research program, is ~35 km long, stretching from the Ross Sea to the polar plateau. Taylor Valley has three hydrologically distinct lake basins that have different soils: Lake Fryxell Basin, nearest the coast; Lake Hoare Basin, intermediate; and Lake Bonney Basin, nearest the polar plateau (for a detailed description see Fountain et al. 1999; Barrett et al. 2004). Fryxell Basin (hereafter Fryxell) has young soil containing relatively high levels of organic carbon and phosphorus, and low salinity, compared to other dry valley soils (Barrett et al. 2007). In contrast, Bonney Basin (hereafter Bonney) has older soils with low levels of organic carbon and phosphorus, and high salinity (Barrett et al. 2007).

Since water is an important determinant of ecosystem structure in the dry valleys and water availability may be altered by climate change (Foreman et al. 2004; Chapman and Walsh 2007; Barrett et al. 2008b), we performed a snow manipulation study to assess how snow accumulation influences soil properties. This was achieved by establishing two snow fences in Taylor Valley, one near Lake Fryxell and the other near Lake Bonney. Soil biochemistry and animal populations were monitored over 5 years along a gradient of increasing snow depth away from the fences. We hypothesized that increased snow depth would be associated with increased soil moisture, decreased salinity and inorganic nitrogen due to leaching, and increased chlorophyll *a* concentrations in the surface soil. In addition, we expected that increased soil moisture would reduce abundances of the microbial feeder *S. lindsayae*, which is most abundant in dry soil, and increase the algal feeder *Eudorilaimus* sp., which is most abundant in moist soil (Treonis et al. 1999; Ayres et al. 2007; Wall 2007). We also expected larger responses of chlorophyll *a* and animal abundances at Fryxell basin than at Bonney basin because water availability likely limits soil biota at Fryxell where soil salinity is relatively low and organic matter concentrations are relatively high, whereas, at Bonney, the high salinity may constrain soil biota more than water availability.

Materials and methods

This study was conducted in Taylor Valley (77°S, 163°E) in the McMurdo Dry Valleys, Antarctica. This region has a polar desert climate with a mean annual temperature of around -19°C and 10–50 mm water equivalent annual precipitation, entirely as snow (Fountain et al. 1999, 2009). The landscape consists of perennially ice-covered lakes, glaciers, and bare soils interspersed with ephemeral streams.

In January 2001 a 6.1 m long snow fence (1 m high) made of coarse plastic mesh was erected on the south side of Lake Fryxell (77.60843°S, 163.24860°E) and on the south side of the west lobe of Lake Bonney (77.72472°S, 162.31309°E) on a flat area of land broadly representative of the surrounding landscape. To collect the most blowing snow, the fences were positioned perpendicular to the long axis of the valley and to the katabatic winds that come from the polar plateau southwest of Taylor Valley (Fountain et al. 1999; Doran et al. 2002a). Environmental regulations placed on field experiments in the dry valleys determined fence size and replication.

Soil samples were collected immediately prior to the establishment of the snow fences, which represent year 0 conditions. Samples were collected along six transects,

perpendicular to each fence on the leeward side, that were evenly spaced ~ 1.5 m apart along the fences (Fig. 1). Along each transect, samples were collected at 0.9, 1.8, 2.7, and 3.7 m away from the fence (Fig. 1). Soil samples were collected in two stages. First, the surface soil (1–2 mm) was collected using plastic spoons and stored in opaque plastic bottles for chlorophyll *a* analysis (a representation of standing photosynthetic biomass). Second, soil was collected from the same location to a depth of 10 cm using plastic scoops. Previous results have shown that surface soils (0–2.5 cm) contain few invertebrates (Powers et al. 1995). Different clean plastic scoops were used to collect each sample to avoid cross contamination. The distances away from the fence were chosen to correspond to an expected gradient of increasing snow depth with distance from the fence based upon the depth of natural snowpacks found on the leeward side of obstacles in the dry valleys (Gooseff et al. 2003). Soil samples were also collected from locations adjacent to previous sampling sites in January (peak of the austral summer) 2, 3, and 5 years after the snow fences were erected (i.e. 2003, 2004, and 2006).

At Fryxell, the depth of the snowpack was measured in November in years 2, 3, 4, 5 and 6 after the snow fence was established (i.e. 2002, 2003, 2004, 2005, and 2006) and in December 2002 and 2003. Along nine transects, spaced 1 m apart and perpendicular to the fences, snowpack depth was determined at nine locations between 1 and 16 m from the fence on the leeward side (Fig. 1). At Bonney snowpack depth was measured in a similar fashion, but only in November 2002 due to logistical difficulties and the general absence of snow during sampling times. In addition to the spatial snow depth measurements, a sonic ranger (Campbell Scientific, Logan, UT, USA) attached to a meteorological station located at the center of each fence recorded snow depth at a single location 1 m from each fence on the leeward side between 2003 and 2006. Snow depth was recorded every 15 min and mean daily snow depths were calculated.

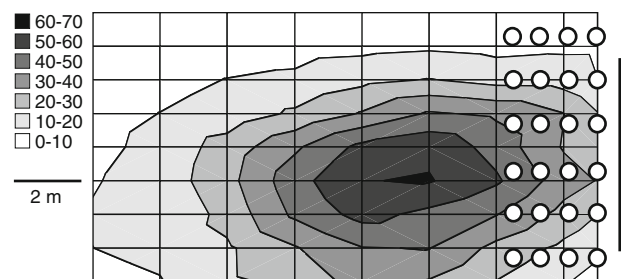


Fig. 1 Mean snow depth (cm) across all sampling dates at Fryxell. Circles represent soil sampling sites; thick black line on the right represents the snow fence. Snowpack depth exhibited a similar pattern at Bonney, but was not as deep (see Fig. 2b)

After collection, soil samples were returned to the laboratory at McMurdo Station and stored at 4°C. Soil fauna were extracted within 48 h using a modified sugar-centrifugation approach (Freckman and Virginia 1993). Nematodes were identified to species, life stage (juvenile or adult), sex, and live or dead. Rotifers and tardigrades were also counted, but not identified further. Gravimetric soil moisture was determined after drying soil (105°C) for 48 h. Soil pH (1:2 soil:deionized water) and electrical conductivity (EC) (1:5 soil:deionized water) were measured using a glass electrode (Orion, Waltman, MA, USA) and a conductivity meter (Corning, Corning, NY, USA), respectively. Concentrations of nitrate and ammonium in 2.0 M KCl extracts were determined on a Lachat Autoanalyzer. Soil was processed at very low light levels for chlorophyll *a* analysis and prepared using an acetone extraction procedure (Powers et al. 1998). Chlorophyll *a* concentration was measured using a Turner model 111 fluorometer (Turner, Palo Alto, CA, USA). Biological and chemical properties are expressed relative to soil dry weight.

We used analysis of variance (ANOVA) to examine the influence of the main effects of lake basin, sampling date, distance from the fence, block (transect), and their interactions on soil biological and chemical properties. Where significant main effects of sampling date or distance were observed, post hoc Tukey HSD tests were applied. For clarity and brevity, effects of block (transect) are not reported in Tables 1, 2, and 3. Soil animal abundances, soil moisture,

Table 1 *F* values relating to the effect of distance from snow fence and sampling date on snow depth from ANOVAs

	Fryxell snow depth	Bonney snow depth
Distance	114.2***	4.1**
Date	442.3***	
Distance × date	4.4***	

Snow depth was only measured at one sampling date at Bonney
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

soil pH, and chlorophyll *a* were $\log(n + 1)$ transformed prior to analysis to meet assumptions of normality and homogeneity of variance.

Results

At the Fryxell fence, snow depth varied among the sampling dates, with the greatest depths observed in November 2006 (Table 1; Fig. 2a). Snow depth decreased quickly as peak austral summer approached, which can be seen in the change in depth between November and December (Figs. 2a, 3). Snow depth at Bonney was only measured in November 2002 and was markedly lower than at Fryxell at the same sampling date (Fig. 2a). Automated snow depth measurements from each snow fence between 2003 and 2006 confirmed substantially lower snow accumulation at

Table 2 *F* values relating to the effect of hydrologic basin, sampling date, and distance from snow fence on soil moisture, electrical conductivity (EC), pH, ammonium, nitrate, and chlorophyll *a* from ANOVAs

	Moisture content	pH	EC	Ammonium	Nitrate	Chlorophyll <i>a</i>
Basin	2467.8***	1387.1***	5496.6***	126.0***	691.9***	92.1***
Date	125.9***	164.7***	6.0**	17.0***	10.4***	303.3***
Distance	2.3	6.6***	3.3*	0.3	4.8**	1.0
Basin × date	110.9***	213.6***	18.1***	40.3***	5.8**	11.1***
Basin × distance	2.3	4.5**	8.1***	1.3	5.5**	3.1*
Date × distance	1.0	0.9	0.6	0.4	0.7	0.6
Basin × date × distance	1.0	1.0	0.5	0.7	0.8	1.7

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3 *F* values relating to the effect of sampling date and distance from snow fence on soil animal populations from ANOVAs, Fryxell basin only; animal occurrences at Bonney were too low to analyze statistically

	<i>S. lindsayae</i> adults	<i>S. lindsayae</i> juveniles	<i>S. lindsayae</i> dead:live	<i>S. lindsayae</i> males:females	<i>Eudorylaimus</i> sp. adults	<i>Eudorylaimus</i> sp. juveniles
Date	16.7***	35.1***	49.6***	14.0***	1.3	16.7***
Distance	2.3	3.1*	0.9	0.5	5.2**	2.2
Date × distance	1.1	0.6	0.6	0.3	1.1	1.2

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

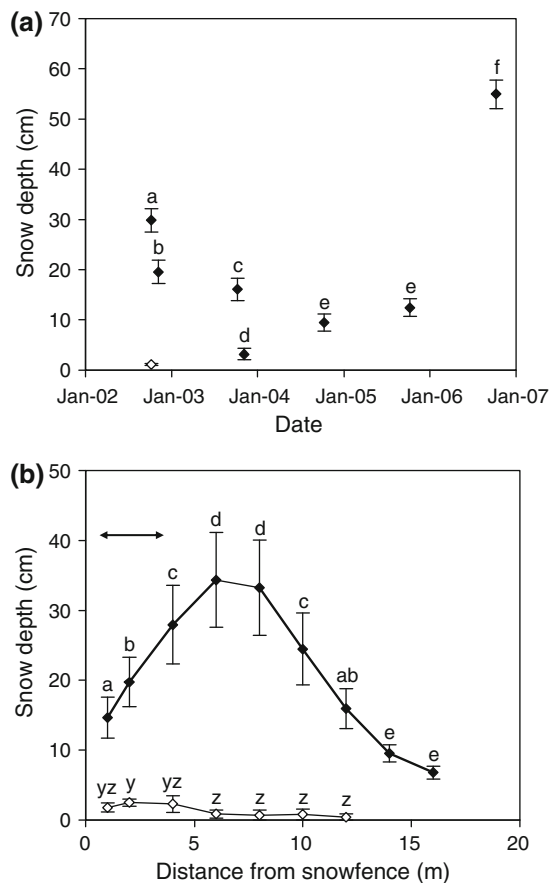


Fig. 2 Mean \pm SE snow depth **a** at sampling dates between November 2002 and December 2006 or **b** with distance from the snow fence across all sampling dates. Solid diamonds represent Fryxell and open diamonds represent Bonney. Different letters within a site denote significant difference ($P < 0.05$). The double-ended arrow denotes the beginning and end of the soil transects

Bonney than Fryxell (Fig. 3). At both sites snow depth initially increased with distance and then decreased (Table 1; Fig. 2b) as is typical for snow fences. Along the soil sampling transects (0.9–3.7 m), a subsection of the total snow accumulation zone, snow depth increased with distance from the fence, such that snow was about twice as deep at the sampling site farthest from the fence (Figs. 1, 2b). Mean (\pm SE) density of the accumulated snow was $0.37 (\pm 0.03)$ g cm^{-3} across all sampling dates and both sites.

Although distance from the snow fence significantly affected some soil characteristics (Tables 2, 3), the interaction between distance and year was never significant, indicating that increased snow depth with distance from the snow fence did not alter soil characteristics from the baseline conditions observed in year 0. Initial soil moisture was greater at Fryxell than at Bonney, and at Fryxell soil moisture was much greater at the later sampling dates than in year 0 (Table 2; Fig. 4a, b), suggesting that the snow trapped by the snow fence increased soil moisture throughout the

entire sampling area. In contrast, soil moisture at Bonney was similar before and after the establishment of the snow fence (Fig. 4b). Soil pH decreased over time at Fryxell, but increased over time at Bonney (Table 2; Fig. 4c, d). EC, a measure of soil salinity, was substantially greater at Bonney than Fryxell, and at Fryxell EC was lowest in years 2 and 3, whereas at Bonney it was greatest in years 2 and 3 (Table 2; Fig. 4e, f).

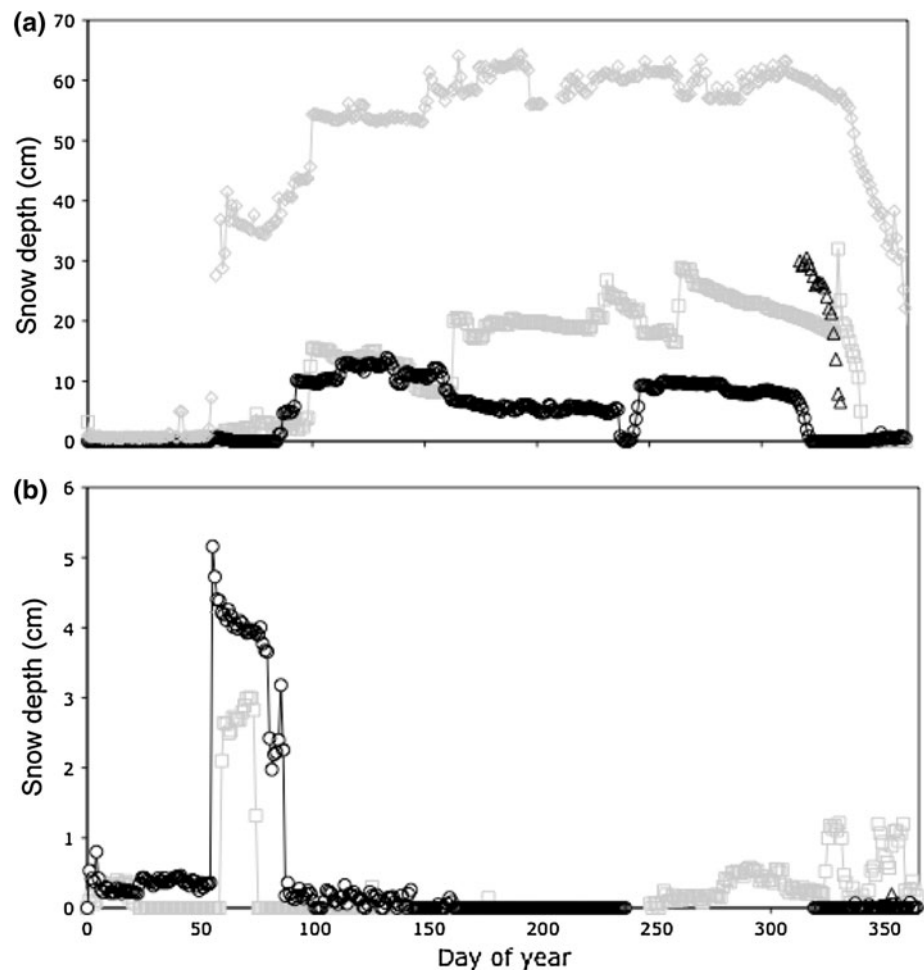
Soil ammonium concentrations were initially similar at Bonney and Fryxell, but at Fryxell they increased over time while at Bonney they decreased over time (Table 2; Fig. 5a, b). Soil nitrate concentrations were an order of magnitude greater at Bonney than Fryxell, and at both basins they decreased in year 2 and increased in year 3 (Table 2; Fig. 5c, d). The concentration of chlorophyll *a* in the surface soil was greater at Fryxell than Bonney, and in both basins chlorophyll *a* was greatest in year 3 and below detection limits in year 0 (Table 2; Fig. 6).

Live *S. lindsayae*, the dominant animal in this ecosystem, and *Eudorylaimus* sp. individuals were found in 100 and 95% of samples at Fryxell, respectively, whereas, at Bonney they were found in only 12 and 0% of samples, respectively. *P. murrayi*, tardigrades, and rotifers were found infrequently (<6% of samples) at both sites. As a result, only abundances of *S. lindsayae* and *Eudorylaimus* sp. at Fryxell could be analyzed statistically. Abundances of live adult and juvenile *S. lindsayae* declined by over 45% at all sampling dates when compared to their initial abundances (Table 3; Fig. 7a, b). This corresponded to a marked increase in the ratio of dead to living (an index of mortality) *S. lindsayae* from over 40 live individuals per dead individual to around 4 live individuals per dead individual (Table 3; Fig. 7c). The ratio of male to female *S. lindsayae* exhibited much variation over the duration of the experiment, being close to 1:1 in years 0 and 5, but below 1:1 in year 2 and >1:1 in year 3 (Table 3; Fig. 7d). The abundance of juvenile *Eudorylaimus* sp. increased fourfold over the course of the experiment, however, the abundance of adults did not differ among the sampling dates (Table 3; Fig. 8). Ratios of dead to living *Eudorylaimus* sp. individuals or males to females in a soil sample often could not be calculated due to their lower abundances.

Discussion

Desert ecosystems, such as the McMurdo Dry Valleys in Antarctica, may be sensitive to changes in snowpack or water availability that could be caused by altered precipitation regime or increased melting as a result of ongoing climate change (Foreman et al. 2004; Chapman and Walsh 2007; Barrett et al. 2008b). To investigate this, we assessed the response of soil properties and animal populations to

Fig. 3 Daily average snow depth at a single location adjacent to the snow fence at **a** Fryxell and **b** Bonney in 2003 (*black triangles*), 2004 (*gray squares*), 2005 (*black circles*), and 2006 (*gray diamonds*). No data were available at Bonney during 2006 and breaks in the data represent failure of the system, which can only be maintained between late October and early February. Note difference in scale



experimentally increased snow accumulation at Fryxell and Bonney. Snowpack depth was substantially greater at Fryxell than Bonney, which is consistent with other snow accumulation studies (Fountain et al. 1999, 2009). Strong katabatic winds frequently blow down-valley in Taylor Valley (i.e. from Bonney to Fryxell) during winter redistributing local snow down-valley where it accumulates on the leeward side of the snow fences (Nylen et al. 2004). That the fence at Bonney had nearly an order of magnitude less snow accumulation than at Fryxell is due to a number of reasons, including an order of magnitude less snowfall, as well as warmer air temperatures, higher winds, and lower relative humidity, which result in elevated sublimation rates (Fountain et al. 1999; Doran et al. 2002a).

Snow density was 0.37 g cm^{-3} , thus a snow depth of $\sim 270 \text{ mm}$ is equivalent to $\sim 100 \text{ mm}$ water. Snow accumulation is about 30 mm water equivalent at Fryxell and about 10 mm water equivalent at Bonney for the entire year (Fountain et al. 2009). Therefore, the snow accumulation at the fence represented a local increase in snow of at least 200% at Fryxell, and perhaps 100% at Bonney. However,

in no cases did distance from the snow fence alter soil properties relative to baseline conditions observed in year 0, i.e. there were no significant distance \times year interactions. This suggests that the depth of the snowpack at the beginning of the austral summer had little impact on mid-summer soil biochemistry and animal populations. In contrast, studies in other ecosystems have observed changes in summer soil properties in response to increased winter snowpack. For example, increased snow accumulation caused by fences at the Toolik Lake Long Term Ecological Research Site, Alaska, increased summer soil nitrogen mineralization rates in a tussock tundra ecosystem, but not in a dry heath ecosystem (Schimel et al. 2004). In a US northern hardwood forest at the Hubbard Brook Experimental Forest, experimental reductions in snow depth stimulated nitrate availability in stands of sugar maple, but not yellow birch (Goffman et al. 2001). Other studies have reported changes in plant or microbial activity, growth, or community structure in response to altered snow accumulation (Walker et al. 1999; Wipf et al. 2006; Buckeridge and Grogan 2008). Had we measured soil parameters at the beginning of the austral summer when snow was present

Fig. 4 Mean \pm SE **a, b** soil moisture, **c, d** soil pH, and **e, f** soil electrical conductivity at **a, c, e** Fryxell and **b, d, f** Bonney across four sampling dates. *Solid line* (year 0), *dashed dotted line* (year 2), *dashed line* (year 3), and *dotted line* (year 5). Note differences in scale between **a, b** and **e, f**

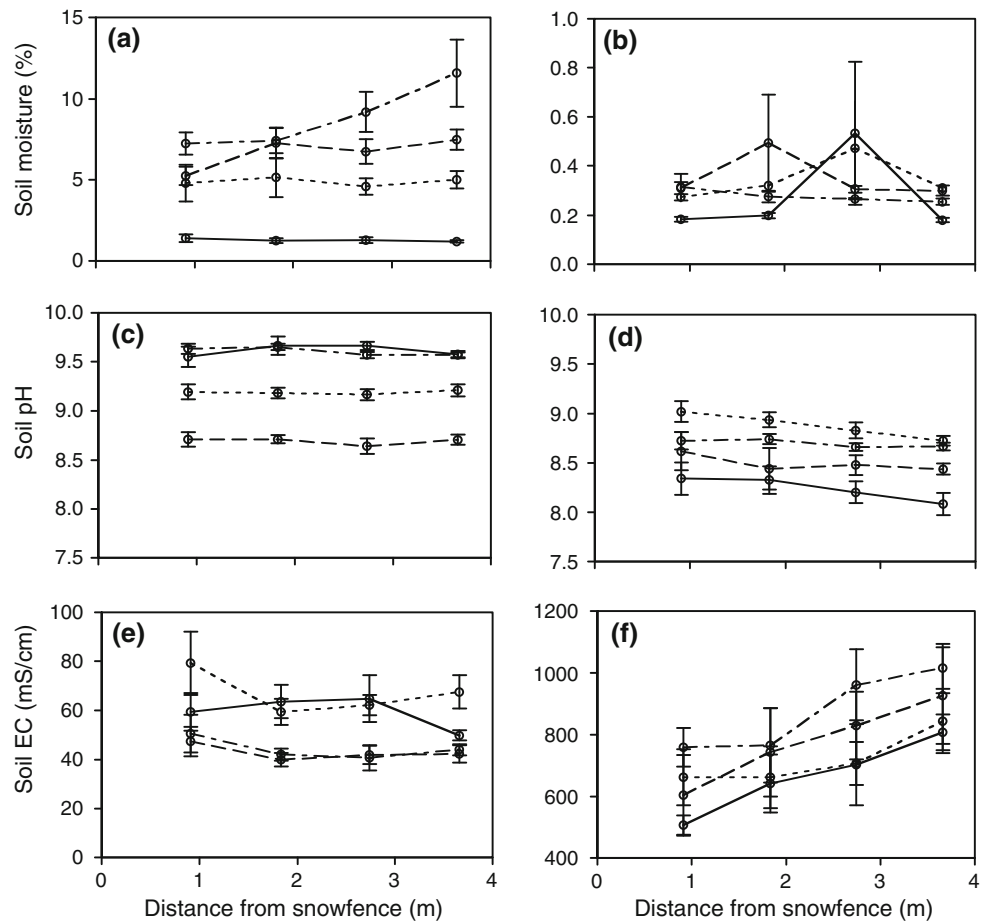
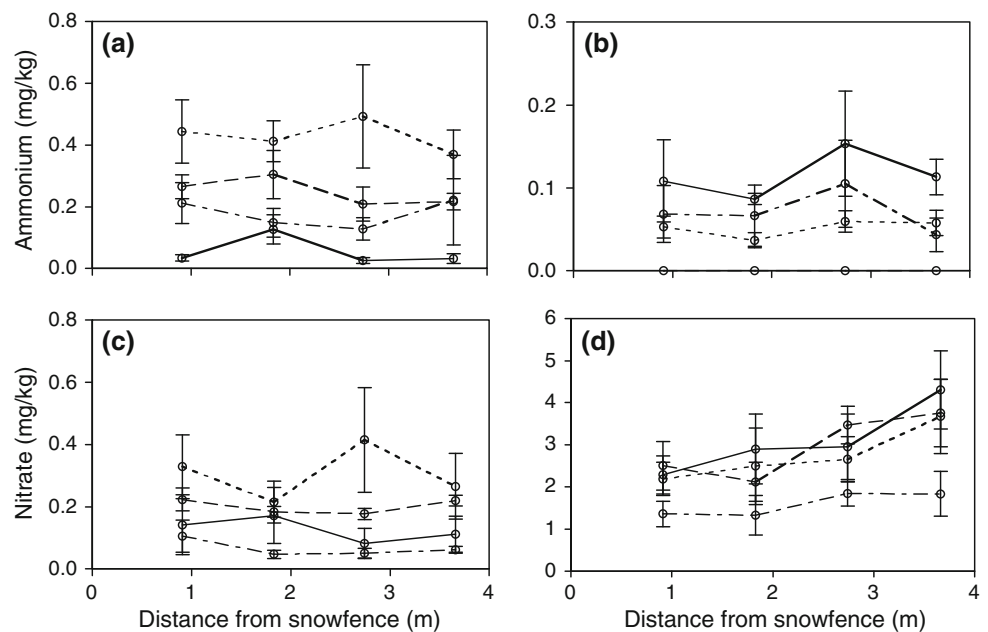


Fig. 5 Mean \pm SE **a, b** soil ammonium, and **c, d** soil nitrate at **a, c** Fryxell and **b, d** Bonney across three sampling dates. *Solid line* (year 0), *dashed dotted line* (year 2), *dashed line* (year 3), and *dotted line* (year 5). Ammonium concentrations at Bonney were below detection limits in year 3. Note differences in scale



we may have seen a relationship between snowpack depth and soil properties resulting from the insulating properties of snow, as found in other studies (Schimel et al. 2004; Kaste et al. 2008).

At least at Fryxell, the additional snow as a result of the snow fence appeared to alter the entire area that was sampled as part of this study. For instance, soil moisture increased from 1 to 5–9% after the snow fence was

Fig. 6 Mean \pm SE chlorophyll *a* at **a** Fryxell and **b** Bonney across three sampling dates. Dashed dotted line (year 2), dashed line (year 3), and dotted line (year 5); chlorophyll *a* was below detection limits in year 0. Note difference in scale

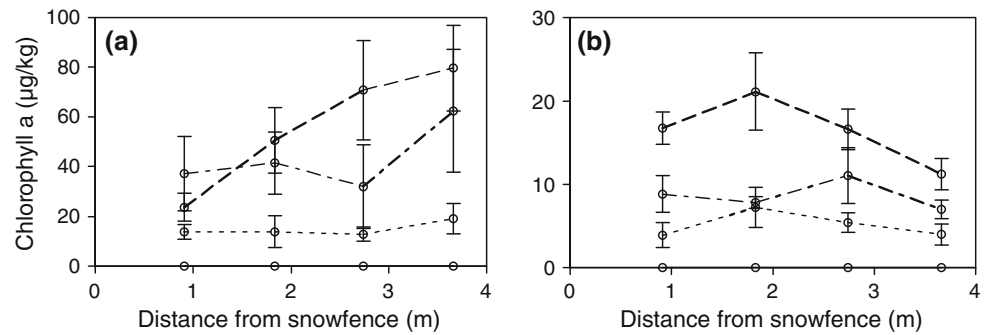
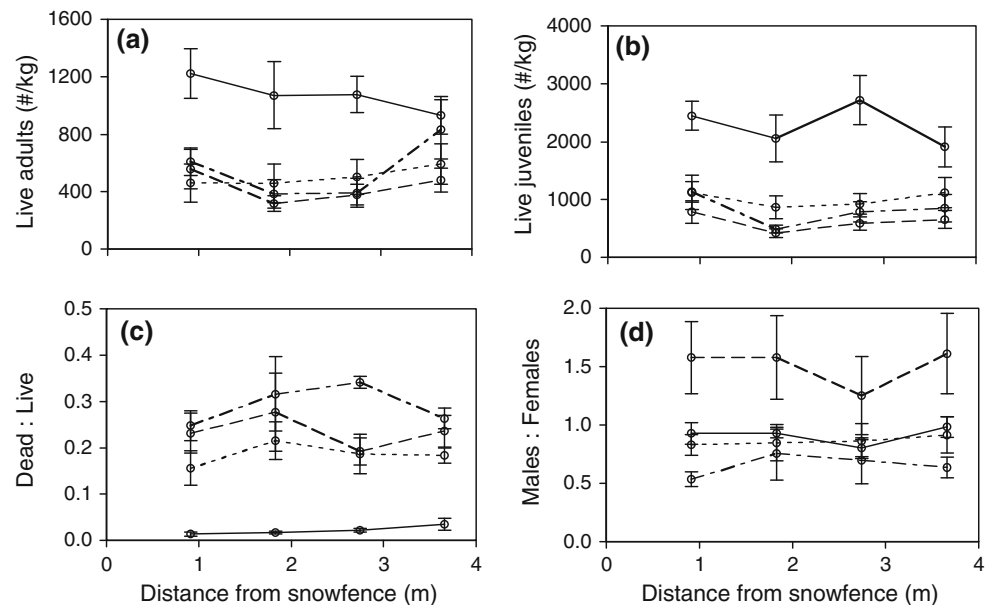


Fig. 7 Mean \pm SE **a** adult abundance, **b** juvenile abundance, **c** ratio of dead to living individuals, and **d** ratio of males to females of *S. lindsayae* at Fryxell across four sampling dates. Solid line (year 0), dashed dotted line (year 2), dashed line (year 3), and dotted line (year 5)



established, and this increase was unrelated to distance from the fence presumably because the water vapor and/or melt-water could easily move through the sandy soil. This is consistent with an observational study of snow patches in Taylor Valley, where soil moisture was 9.4% beneath snow patches and 0.4% in nearby exposed soil (Gooseff et al. 2003). Other studies located near our sampling site at Fryxell have reported soil moisture values similar to the baseline values we observed (Barrett et al. 2004); whereas the higher values we observed at the later sampling dates have only been found in wetted regions surrounding lakes and streams (Treonis et al. 1999; Ayres et al. 2007), indicating that as the snow sublimated and/or melted it increased soil moisture across the entire area that we sampled, not simply directly below where it accumulated. In contrast, at Bonney soil moisture content was low and did not differ before and after the snow fence was established, presumably due to much lower snow accumulation at that site. However, since the fence at Bonney did accumulate some snow, it is possible that soil moisture also increased at Bonney in early summer, but to a lesser degree than at Fryxell.

The increase in soil moisture after the snow fence was established at Fryxell corresponded to decreased abundances of live *S. lindsayae*, increased numbers of dead *S. lindsayae*, and increased abundances of *Eudorylaimus* sp. juveniles. This is consistent with an observational study of animal abundance in soil beneath snow patches and neighboring exposed soil, which reported lower abundances of *S. lindsayae* and greater abundances of *Eudorylaimus* sp. beneath snow patches (Gooseff et al. 2003). Similarly, *Eudorylaimus* sp. increased in abundance in response to a major melting event in the 2001–2002 austral summer, caused by above average air temperatures, that resulted in increased soil moisture (Barrett et al. 2008b). In addition, the availability of water has been shown to strongly influence nematode activity, abundance, and community structure in arid ecosystems at lower latitudes (Freckman et al. 1987; Alon and Steinberger 1999; Bakonyi and Nagy 2000; Bakonyi et al. 2007) as well as in Antarctic dry valleys (Treonis et al. 2000).

The shift in the relative abundance of *S. lindsayae* versus *Eudorylaimus* sp. that we observed at Fryxell was substantial. Initially there were 114 live *S. lindsayae* individuals

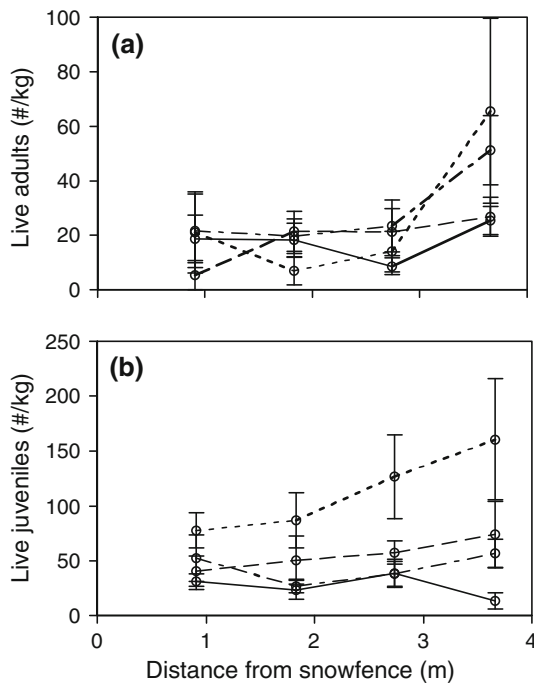


Fig. 8 Mean \pm SE **a** adult abundance and **b** juvenile abundance of *Eudorylaimus* sp. at Fryxell across four sampling dates. Solid line (year 0), dashed dotted line (year 2), dashed line (year 3), and dotted line (year 5). The lower abundance of *Eudorylaimus* sp. meant that ratios of dead to living individuals or males to females in a soil sample often could not be calculated

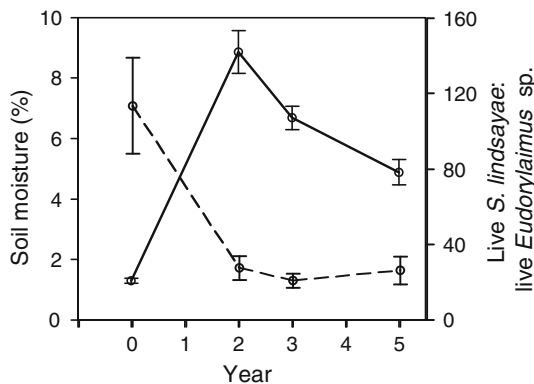


Fig. 9 Change in mean \pm SE soil moisture (solid line) and the relative abundance of live *S. lindsayae* and *Eudorylaimus* sp. (dashed line) at Fryxell over the course of the experiment

for every *Eudorylaimus* sp. individual, but this decreased to between 21:1 and 27:1 after the snow fence was established (Fig. 9). While general declines in *S. lindsayae* have been observed throughout Taylor Valley, which have been linked to regional climate cooling (Doran et al. 2002b; Barrett et al. 2008a), the decline we observed was more precipitous; *S. lindsayae* declined by ~60% over the first 2 years of the experiment and subsequently remained relatively

stable, whereas the decline observed by Doran et al. (2002b) was equivalent to a ~10% reduction per year. The decrease in *S. lindsayae* and increase in *Eudorylaimus* sp. were probably caused by the increase in soil moisture as a result of the snow fence. *S. lindsayae* is most abundant in dry soil in the McMurdo Dry Valleys (Freckman and Virginia 1997; Barrett et al. 2004; Adams et al. 2006), whereas, it sharply decreases in abundance with increased soil moisture, as seen along transects from dry soil to wetter regions surrounding lakes and streams (Treonis et al. 1999; Moorhead et al. 2003; Ayres et al. 2007). In contrast, *Eudorylaimus* sp. is more abundant in moist areas than in drier soils (Powers et al. 1998; Treonis et al. 1999; Porazinska et al. 2002; Ayres et al. 2007). For example, in dry soil at Fryxell, Barrett et al. (2004) reported ~140 *S. lindsayae* individuals for every *Eudorylaimus* sp., whereas in moist soils on the shore of Lake Fryxell Ayres et al. (2007) reported ~3 *S. lindsayae* for every *Eudorylaimus* sp. Over greater time periods we predict that adult *Eudorylaimus* sp. would also increase in abundance. The generation time of *Eudorylaimus* sp. is unknown; however, *S. lindsayae* requires 218 days at 10°C to reach maturity (Overhoff et al. 1993), which would take several years given the climate in this ecosystem. It is reasonable to assume that the life cycle of *Eudorylaimus* sp. also spans several years given the short austral summer and the long lifespan of other Dorylaimidae species (e.g. Coiro et al. 1995), therefore, any change in the abundance of adults may take several years to appear.

It is difficult to determine if variation that we observed in many other soil variables over the course of the experiment was caused by increased water availability, as a result of snow accumulation by the snow fence, or simply represent temporal variation related to another factor. For instance, it is possible that the increase in chlorophyll *a*, which was below detection limits when the fence was erected, may have been a response to increased water availability, since chlorophyll *a* concentrations are often greater in moist soil (Ayres et al. 2007) than in dry soil (Barrett et al. 2004). However, several of the soil parameters we measured exhibit temporal variation in this ecosystem (Porazinska et al. 2002; Simmons et al. 2009), therefore, the changes we observed may simply reflect variation in response to another factor, rather than impacts of snow accumulation, such as summer temperatures (Barrett et al. 2008a, b).

The differences in soil properties and biota that we observed between Fryxell and Bonney were in line with previous studies. Soil pH, and abundances of *S. lindsayae* and *Eudorylaimus* sp. have previously been shown to be greater at Fryxell than Bonney, while EC (salinity) and nitrate concentrations exhibit the opposite pattern, and these differences have been attributed to geologic and climatic legacies (Fountain et al. 1999; Barrett et al. 2004; Ayres et al. 2007).

In conclusion, differences in early summer snowpack depth had little direct effect on mid-summer soil properties. However, at Fryxell, which had the greatest snow accumulation, elevated snow accumulation increased soil moisture throughout the entire experimental area. This coincided with a substantial decline in *S. lindsayae* populations, the dominant animal in this ecosystem, and an increase in abundance of *Eudorylaimus* sp., which is more abundant in moist soils. Changes in other soil parameters, e.g. chlorophyll *a* concentration, may have also resulted from increased soil moisture or may simply represent temporal variation in response to other factors. If climate change does alter snow accumulation in this ecosystem in the future, our findings suggest that as well as altering the hydrological cycle, the community composition of the dominant animals may also change, which in turn may alter biogeochemical cycling (Barrett et al. 2008a).

Acknowledgments Snow depth and density measurements were performed by Thomas Nylen and Hassan Basagic. Steve Blecker, Holley Zadeh, Claire Ojima, Andy Parsons, Dorota Porazinska, and Emma Broos assisted with soil sample collection and processing. This study was supported by National Science Foundation grants OPP 9810219 and OPP 0096250 as part of the McMurdo Dry Valley LTER.

References

- Adams BJ, Bardgett RD, Ayres E, Wall DH, Aislabie J, Bamforth S, Bargagli R, Cary C, Cavacini P, Connell L, Convey P, Fell JW, Frati F, Hogg ID, Newsham KK, O'Donnell A, Russell N, Seppelt RD, Stevens MI (2006) Diversity and distribution of Victoria Land biota. *Soil Biol Biochem* 38:3003–3018
- Alon A, Steinberger Y (1999) Response of the soil microbial biomass and nematode population to a wetting event in nitrogen-amended Negev desert plots. *Biol Fertil Soils* 30:147–152
- Andrassy I (1998) Nematodes in the sixth continent. *J Nematode Morphol Syst* 1:107–186
- Andrassy I (2008) *Eudorylaimus* species (Nematoda: Dorylaimida) of continental Antarctica. *J Nematode Morphol Syst* 11:49–66
- Ayres E, Wall DH, Adams BJ, Barrett JE, Virginia RA (2007) Unique similarity of faunal communities across aquatic-terrestrial interfaces in a polar desert ecosystem. *Ecosystems* 10:523–535
- Bakonyi G, Nagy P (2000) Temperature- and moisture-induced changes in the structure of the nematode fauna of a semiarid grassland—patterns and mechanisms. *Glob Chang Biol* 6:697–707
- Bakonyi G, Nagy P, Kovacs-Lang E, Kovacs E, Barabas S, Repasi V, Seres A (2007) Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. *Appl Soil Ecol* 37:31–40
- Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature* 438:303–309
- Barrett JE, Virginia RA, Wall DH (2002) Trends in resin and KCl-extractable soil nitrogen across landscape gradients in Taylor Valley, Antarctica. *Ecosystems* 5:289–299
- Barrett JE, Virginia RA, Wall DH, Parsons AN, Powers LE, Burkins MB (2004) Variation in biogeochemistry and soil biodiversity across spatial scales in a polar desert ecosystem. *Ecology* 85:3105–3118
- Barrett JE, Virginia RA, Lyons WB, McKnight DM, Priscu JC, Doran PT, Fountain AG, Wall DH, Moorhead DL (2007) Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. *J Geophys Res Biogeosci* 112:G01010
- Barrett JE, Virginia RA, Wall DH, Adams BJ (2008a) Decline in a dominant invertebrate species contributes to altered carbon cycling in a low-diversity soil ecosystem. *Glob Chang Biol* 14:1–11
- Barrett JE, Virginia RA, Wall DH, Doran PT, Fountain AG, Welch KA, Lyons WB (2008b) Persistent effects of a discrete warming event on a polar desert ecosystem. *Glob Chang Biol* 14:2249–2261
- Buckeridge KM, Grogan P (2008) Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. *Appl Soil Ecol* 39:210–222
- Campbell IB (2003) Soil characteristics at a long-term ecological research site in Taylor Valley, Antarctica. *Aust J Soil Res* 41:351–364
- Campbell IB, Claridge GGC (1987) Antarctica: soils, weathering processes and environment. Elsevier, Amsterdam
- Cannone N, Wagner D, Hubberten HW, Guglielmin M (2008) Biotic and abiotic factors influencing soil properties across a latitudinal gradient in Victoria Land, Antarctica. *Geoderma* 144:50–65
- Chapman WL, Walsh JE (2007) A synthesis of Antarctic temperatures. *J Clim* 20:4096–4117
- Chinn TH (1993) Physical hydrology of the dry valley lakes. In: Green WJ, Friedmann EI (eds) Physical and biogeochemical processes in Antarctic lakes. American Geophysical Union, Washington, DC, pp 1–51
- Coiro MI, Sasanelli N, Serino M (1995) Fecundity and longevity of individual *Xiphinema ifacolum* (Nematoda, Dorylaimidae) on tomato. *Nematologica* 41:191–196
- Connell L, Redman R, Craig S, Rodriguez R (2006) Distribution and abundance of fungi in the soils of Taylor Valley, Antarctica. *Soil Biol Biochem* 38:3083–3094
- Doran PT, McKay CP, Clow GD, Dana GL, Fountain AG, Nylen T, Lyons WB (2002a) Valley floor climate observations from the McMurdo dry valleys, Antarctica, 1986–2000. *J Geophys Res Atmos* 107:4772
- 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 (2002b) Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415:517–520
- Elberling B, Gregorich EG, Hopkins DW, Sparrow AD, Novis P, Greenfield LG (2006) Distribution and dynamics of soil organic matter in an Antarctic dry valley. *Soil Biol Biochem* 38:3095–3106
- Fell JW, Scorzetti G, Connell L, Craig S (2006) Biodiversity of micro-eukaryotes in Antarctic Dry Valley soils with <5% soil moisture. *Soil Biol Biochem* 38:3107–3119
- Foreman CM, Wolf CF, Priscu JC (2004) Impact of episodic warming events on the physical, chemical and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquat Geochem* 10:239–268
- Fountain AG, Lyons WB, Burkins MB, Dana GL, Doran PT, Lewis KJ, McKnight DM, Moorhead DL, Parsons AN, Priscu JC, Wall DH, Wharton RA, Virginia RA (1999) Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience* 49:961–971
- Fountain AG, Nylen TH, Monaghan A, Basagic HJ, Bromwich D (2009) Snow in the McMurdo Dry Valleys, Antarctica. *Int J Climatol*. doi:10.1002/joc.1933
- Freckman DW, Virginia RA (1993) Extraction of nematodes from Dry Valley Antarctic soils. *Polar Biol* 13:483–487
- Freckman DW, Virginia RA (1997) Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. *Ecology* 78:363–369

- Freckman DW, Virginia RA (1998) Soil biodiversity and community structure in the McMurdo Dry Valleys, Antarctica. In: Prisco JC (ed) Ecosystem dynamics in a polar desert: the McMurdo Dry Valleys, Antarctica. American Geophysical Union, Washington, DC, pp 323–335
- Freckman DW, Whitford WG, Steinberger Y (1987) Effect of irrigation on nematode population-dynamics and activity in desert soils. *Biol Fertil Soils* 3:3–10
- Gooseff MN, Barrett JE, Doran PT, Fountain AG, Lyons WB, Parsons AN, Porazinska DL, Virginia RA, Wall DH (2003) Snow-patch influence on soil biogeochemical processes and invertebrate distribution in the McMurdo Dry Valleys, Antarctica. *Arct Antarct Alp Res* 35:91–99
- Grippa M, Kergoat L, Le Toan T, Mognard NM, Delbart N, L'Hermitte J, Vicente-Serrano SM (2005) The impact of snow depth and snowmelt on the vegetation variability over central Siberia. *Geophys Res Lett* 32:L21412
- Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001) Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. *Biogeochemistry* 56:191–213
- Groffman PM, Hardy JP, Driscoll CT, Fahey TJ (2006) Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. *Glob Chang Biol* 12:1748–1760
- IPCC (2007) Fourth assessment report: climate change 2007. Cambridge University Press, Cambridge
- Kaste O, Austnes K, Vestgarden LS, Wright RF (2008) Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. *Ambio* 37:29–37
- Kennedy AD (1993) Water as a limiting factor in the Antarctic terrestrial environment—a biogeographical synthesis. *Arct Alp Res* 25:308–315
- Moorhead DL, Barrett JE, Virginia RA, Wall DH, Porazinska D (2003) Organic matter and soil biota of upland wetlands in Taylor Valley, Antarctica. *Polar Biol* 26:567–576
- Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in western north America. *Bull Am Meteorol Soc* 86:39
- Nylen TH, Fountain AG, Doran PT (2004) Climatology of katabatic winds in the McMurdo dry valleys, southern Victoria Land, Antarctica. *J Geophys Res Atmos* 109:D03114
- Overhoff A, Freckman DW, Virginia RA (1993) Life cycle of the microbivorous Antarctic Dry Valley nematode *Scottinema lindsayae* (Timm 1971). *Polar Biol* 13:151–156
- Poage MA, Barrett JE, Virginia RA, Wall DH (2008) The influence of soil geochemistry on nematode distribution, McMurdo Dry Valleys, Antarctica. *Arct Antarct Alp Res* 40:119–128
- Porazinska DL, Wall DH, Virginia RA (2002) Population age structure of nematodes in the Antarctic Dry Valleys: perspectives on time, space, and habitat suitability. *Arct Antarct Alp Res* 34:159–168
- Powers LE, Freckman DW, Virginia RA (1995) Spatial distribution of nematodes in polar desert soils of Antarctica. *Polar Biol* 15:325–333
- Powers LE, Ho MC, Freckman DW, Virginia RA (1998) Distribution, community structure, and microhabitats of soil invertebrates along an elevational gradient in Taylor Valley, Antarctica. *Arct Alp Res* 30:133–141
- Schimel JP, Bilbrough C, Welker JA (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biol Biochem* 36:217–227
- Schwarz AMJ, Green TGA, Seppelt RD (1992) Terrestrial vegetation at Canada Glacier, Southern Victoria Land, Antarctica. *Polar Biol* 12:397–404
- Simmons BL, Wall DH, Adams BJ, Ayres E, Barrett JE, Virginia RA (2009) Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica. *Soil Biol Biochem* 41:2052–2060
- Stevens MI, Hogg ID (2002) Expanded distributional records of *Collembola* and *Acari* in southern Victoria land, Antarctica. *Pedobiologia* 46:485–495
- Treonis AM, Wall DH, Virginia RA (1999) Invertebrate biodiversity in Antarctic dry valley soils and sediments. *Ecosystems* 2:482–492
- Treonis AM, Wall DH, Virginia RA (2000) The use of anhydrobiosis by soil nematodes in the Antarctic Dry Valleys. *Funct Ecol* 14:460–467
- Ugolini FC, Bockheim JG (2008) Antarctic soils and soil formation in a changing environment: a review. *Geoderma* 144:1–8
- Walker MD, Walker DA, Welker JM, Arft AM, Bardsley T, Brooks PD, Fahnestock JT, Jones MH, Losleben M, Parsons AN, Seastedt TR, Turner PL (1999) Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrol Process* 13:2315–2330
- Wall DH (2007) Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem. *Philos Trans R Soc B Biol Sci* 362:2291–2306
- Wipf S, Rixen C, Mulder CPH (2006) Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Glob Chang Biol* 12:1496–1506