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Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica

B.L. Simmons^{a,*}, D.H. Wall^{a,b}, B.J. Adams^c, E. Ayres^a, J.E. Barrett^d, R.A. Virginia^e

^a Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

^b Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

^c Department of Biology and Evolutionary Ecology Laboratories, Brigham Young University, Provo, UT 84602, USA

^d Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

^e Environmental Studies Program, Dartmouth College, Hanover, NH 03755, USA

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ABSTRACT

Climate models predict significant future warming in polar regions. In the McMurdo Dry Valleys, Antarctica, projected summer climate warming is expected to increase snow and glacial melt, resulting in higher stream discharge, rising lake levels, and an increase in areas of moist soil, but the potential influence of warming and associated changes in hydrology on the soil ecosystem is poorly understood. To examine the effects of soil warming and changes in the availability of liquid water on populations of soil invertebrates and their habitat, we established a full-factorial warming and water addition experiment at one experimental site in each of the three hydrologic basins of Taylor Valley, Antarctica, and measured responses over 8 years. We hypothesized that an increase in temperature and moisture together would enhance habitat suitability for soil invertebrates thereby increasing abundance, biomass and diversity of the soil animal communities. Instead, warming treatments had an overall negative effect on density and body size of the microbial-feeding nematode Scottnema lindsayae, the dominant animal in the dry valleys, which decreased by 42% in warmed plots. While experimental moisture additions as a single annual pulse had no effect on nematodes, the surface flooding of one site from rapid melting of upslope subsurface ice (the result of an unusual natural warming event) drastically altered soil moisture, salinity, and animal communities; mortality of S. lindsayae increased and densities decreased. This extreme soil wetting event also resulted in an increase in chlorophyll a and populations of Eudorylaimus spp, a nematode species that prefers moist to wet habitats and feeds on soil micro-algae. Our results suggest that warming in the dry valleys could significantly affect soil nematode populations and species composition both directly and indirectly by altering species-specific habitat suitability for soil biota.

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1. Introduction

Polar ecosystems are particularly sensitive to climate change, where small changes in temperature result in greater changes in local hydrology, dramatically affecting ecosystem processes (Chapin et al., 2008). As in temperate deserts, polar deserts are very sensitive to alterations in the availability of water to soil food webs (Whitford et al., 1981; Freckman et al., 1987; Austin et al., 2004). Understanding this influence on polar ecosystems requires evaluation of the singular and additive effects of variation in temperature and moisture. Therefore, the polar deserts of Antarctica, where recent climate variation has resulted in both a regional cooling trend (Doran et al., 2002b) and as a discrete seasonal warming

event (Barrett et al., 2008a), are an ideal location for investigating the relationship between climate, soil biodiversity and function in temperature sensitive systems.

The McMurdo Dry Valleys of Antarctica are an ice-free terrestrial landscape consisting of glaciers, ephemeral streams, ice-covered lakes and arid soils that are among the coldest and driest on Earth (Bockheim, 1997), where carbon and biologically available water are major limiting factors for life (Kennedy, 1993; Barrett et al., 2007). Except for mosses and algae that are typically restricted to areas of moisture, visible sources of organic matter are absent. The harsh environment and low availability of carbon and water support a simplified belowground mesofaunal community of rotifers, tardigrades, nematodes, and microarthropods near lakes and ephemeral streams, and even simpler communities in the arid soils that occupy the majority of the landscape (Wall and Virginia, 1999; Wall, 2005; Adams et al., 2006). Soil nematodes in the dry valley region generally represent the apex of two complementary food





^{*} Corresponding author. Tel.: +1 970 491 3552; fax: +1 970 491 1965. *E-mail address:* breana@nrel.colostate.edu (B.L. Simmons).

chains, one based on contemporary algal and moss productivity and one based on decomposition of exogenous lake-derived organic matter (Burkins et al., 2000; Elberling et al., 2006). *Scottnema lindsayae*, a microbial feeder and the most abundant and widely distributed metazoan invertebrate, often occurs as the sole metazoan species in the arid soils of the McMurdo Dry Valleys (Powers et al., 1998; Wall and Virginia, 1999; Bamforth et al., 2005; Wall, 2005). In contrast, all other invertebrate species are more abundant in moist or saturated soils where algae and moss are more abundant (Treonis et al., 1999; Adams et al., 2006; Ayres et al., 2007).

Species abundance, richness and diversity of invertebrate communities are extremely patchy in this system, and vary significantly over scales of meters to kilometers (Courtright et al., 2001; Porazinska et al., 2002; Barrett et al., 2004). Distribution of most species is correlated negatively with elevation (probably the result of an interaction between temperature and precipitation) and salinity, and positively with soil moisture, soil organic matter, and nutrient availability (Freckman and Virginia, 1997; Powers et al., 1998; Poage et al., 2008). Of these variables, salinity controls the distribution of nematodes over both fine and broad scales associated with landscape differences in geomorphology and soil age (Barrett et al., 2004; Nkem et al., 2006; Poage et al., 2008). At finer scales, such as soil polygons, soil invertebrate abundances (with the notable exception of S. lindsayae) are positively correlated with soil moisture, soil carbon, and when salinity is suitable these are likely the most important limiting factors for successful colonization of soils in the dry valleys (Barrett et al., 2004). Therefore, for most invertebrates in this system, optimal habitat suitability would be seasonally moist soils with low salinity and high organic matter content (Freckman and Virginia, 1998; Courtright et al., 2001).

A recent short-duration summer warming event in Taylor Valley resulted in persistent effects on both hydrologic and geochemical properties of soils (Lyons et al., 2005) and soil biota (Barrett et al., 2008b). While studies in the Antarctic Peninsula have documented alterations in community composition of soil microarthropods and nematodes following climate manipulations (Convey et al., 2002), influences of climate warming on dry valley soil faunal populations and soil chemistry are unclear, due partly to the interaction of temperature and water availability. Such information is critical in areas of low biodiversity, which may be more sensitive to climate changes because with little or no functional redundancy the loss or gain of a few species could result in a significant change in ecosystem functioning (Wall, 2007; Barrett et al., 2008a). A warmer, wetter Antarctica would theoretically increase the optimal habitat for most invertebrate species, allowing for a longer periods of growth and activity and possibly increasing the frequency of multiple species communities across the landscape.

Our experiment was designed to test the effect of increased temperature and moisture on the soil biota and soil characteristics in three distinct lake basins in Taylor Valley, Antarctica. We hypothesized that increased temperature and moisture would benefit the soil biota by removing important environmental constraints on their growth and activity, i.e., creating a more suitable habitat. In plots that were warmed and/or wetted over several years, we expected increases in faunal abundance, diversity, number of juveniles per adult female, and body size, as well as a decrease in mortality with greater habitat suitability.

2. Materials and methods

2.1. Site description

The McMurdo Dry Valleys, located in Southern Victoria Land, are the principle region of study for the McMurdo Dry Valleys Long Term Ecological Research program, where average annual temperatures range from -17 to -20 °C, with an average precipitation of less than 100 mm (Doran et al., 2002a). The soils are sandy, alkaline and typically saline (Campbell and Claridge, 1988) with soil organic matter largely derived from contemporary and paleolake sediments (Burkins et al., 2000; Elberling et al., 2006). In December 1999, an experiment was established in three hydrologically distinct lake basins of Taylor Valley, listed from west to east: Bonney (77°43′ S, 162°18′ E), Hoare (77°37′ S, 162°52′ E) and Fryxell (77°38′ S, 163°06′ E). These specific basins were chosen because they represent a gradient of soil properties and suitable habitat for biota, with Fryxell being the most suitable and Bonney being the least suitable (Wall and Virginia, 1999; Barrett et al., 2004). Climate data for the sampling period are summarized in Table 1.

2.2. Experimental design and treatments

In each basin, six blocks were established, each containing four experimental treatments: control (ambient), increased temperature, increased water, and increased temperature and water. Plots with increased water received 12.7 L/m² deionized water once each year starting in December 1999. Water was applied by hand using a plastic carboy modified with a sprinkler cap, bringing the top 10 cm of the soil profile to field capacity. Because low temperatures (frozen soils) prohibit the application of water in multiple pulses over a long season, a larger, single pulse in mid-summer (when soil thaw was greatest) was determined to be more logistically feasible. In plots with increased temperature, International Tundra Experiment (ITEX) open top warming chambers (Marion et al., 1997; Hollister and Webber, 2000) were placed on the soil and secured to the ground. These chambers are conical (0.44 m² internal footprint) with sloping sides constructed of Sun-Lite HP™ fiberglass (Solar Components Corporation, Manchester, NH, USA). The material is 1 mm thick and allows high transmittance of visible wavelengths (86%) and low transmission of infrared wavelengths (<5%), and further traps heat due to the inward angle of the cone.

To provide an estimate of the effect of the chamber on the soil microclimate, comparative data were collected near a long-term experiment on the south side of Lake Hoare. Between 1999 and 2005, thermocouples permanently buried at three depths (0, 5, and 10 cm) in both a chambered and control plot collected temperature observations every 30 s and averaged and stored data at 10-min intervals by a Campbell CR10XT data-logger (Campbell Corporation, Logan UT). Liquid soil water was estimated at 5 cm depth by soil

Table 1

Austral summer temperatures (°C) for both air and soil (average of probes at 0, 5 and 10 cm) from meteorological stations using Campbell Scientific radiation shields (except where indicated) located in three lake basins in Taylor Valley, Antarctica. Temperatures reflect post-processed daily running means collected every 30 s and stored every 10 min. These data were averaged (±standard error) from December 1 to February 28 except in 2006/2007; 2007 data is currently unavailable.

Year		Lake Bonney (West)	Lake Hoare (Central)	Lake Fryxell (East)
1999/2000	Air	-3.72 (0.3)	-5.15(0.4)	-4.67 (0.4)
2001/2002	5011	1.21 (0.4)	-1.17 (0.7)	-1.42 (0.3)
2001/2002	Air Soil	-2.90 (0.4) 2.56 (0.5)	-4.16(0.4) 2.94(0.6) ^a	-4.08(0.4) 0.74(0.4)
2002/2003	Air Soil	-4.60 (0.3) 1.39 (0.4) ^b	-6.02 (3.8) 1.42 (0.4) ^a	-6.02 (0.3) -0.76 (0.3)
2004/2005	Air Soil	$-3.28 (0.4) \\ 2.88 (0.5)^{b}$	-4.52 (0.4) 1.86 (0.6)	-4.46 (0.4) 0.13 (0.4)
2006	Air Soil	-2.99 (0.5) 3.06 (0.2)	-4.31 (0.5) 4.76 (0.4)	-6.56 (0.6) 0.52 (0.3)

^a Data were collected using a data logger and thermocouples adjacent to an existing experiment on the south side of Lake Hoare.

^b Data were collected by a temporary meteorological station on the western lobe of Lake Bonney and reflect surface soil temperatures only.

reflectometry using 2 theta probes (Delta-T Devices, Cambridge, UK). Estimates of gravimetric soil moisture (% g/g) were calculated from the voltage output (ν) of the theta probes as described by Barrett et al. (2008b).

2.3. Soil sampling and analyses

The plots were sampled in each basin during the austral summer of 1999/2000, 2001/2002, 2002/2003, 2004/2005, and 2006/2007 in December or January. Samples taken during the 1999/2000 summer represent pre-treatment conditions. Before adding water, soil samples were collected to a depth of 10 cm (approximately 500 g) using sterile plastic scoops and immediately transferred into sterile plastic bags. Samples were placed in an insulated chest for transport to Crary Laboratory at McMurdo Station, Antarctica. Soils were sub-sampled under a laminar flow hood. Nematodes, tardigrades and rotifers were extracted within 48 h from 100 g sub-samples that were wet sieved and centrifuged in a sugar solution (Freckman and Virginia, 1993). Soil fauna were enumerated under an inverted light microscope ($100-400\times$), and nematodes identified to species and classified by sex, life stage (juvenile/adult) and viability (live/dead). Animal abundance is reported as the number of live organisms per kilogram dry soil. Soil moisture content was determined gravimetrically; sub-samples of soil were dried at 105 °C for 48 h. Soil pH was estimated on 1:2 soil extracts using deionized water on an Orion model 720A pH meter (Orion, Waltham, Massachusetts, USA). Salinity was estimated by measuring electrical conductivity of 1:5 soil deionized water extracts using a Yellow Springs Instrument 3100 conductivity meter (Yellow Springs Instrument Co., Yellow Springs, Ohio, USA). Soils were processed and prepared for chlorophyll *a* analysis, a proxy for soil algal productivity, using an acetone extraction/ fluorometric procedure described by Barrett et al. (2004).

For biomass measurements, up to 10 adult *S. lindsayae* of each sex from each plot at all experimental sites (N = 1464) in 1999/2000 and 2004/2005 were photographed using SPOT 3.0 imaging software for microscope digital cameras (Diagnostics Instruments, Sterling Heights, Michigan, USA). The images were measured (lengths from tail to mouth, widths from just behind the basal pharyngeal bulb) using Carnoy 2.0 digital image analysis program (Lab of Plant Systematics, Katholieke Universiteit Leuven, Flanders, Belgium). Biomass was calculated by determining average individual dry weights from lengths and width and corrected for water content using standard calculations (e.g., Freckman, 1982).

Soil faunal community data and biomass calculations were analyzed as full factorials using the fit model procedure in JMP 5.0 (biomass measurements) or mixed models in SAS 9.0. Temperature and moisture treatments were both included as independent variables to determine if they influenced soils alone or in combination. Animal abundances were transformed (\log_{x+1}) to fit assumptions of normality, and only abundances of live organisms were used for comparisons. If appropriate, post hoc Tukey's HSD test was used to further elucidate differences between basins, years and treatments. Sex ratio (number of living males per living female), number of living juveniles per living female, and mortality (number of dead individuals per living individuals) were calculated for *S. lindsayae* only, because other nematode species were not adequately abundant for these calculations. Significance was assigned at P < 0.05.

3. Results

3.1. Soil properties

The ITEX chambers increased soil surface temperatures by approximately 2 °C between December and February (the austral

summer), and although the effect was less pronounced with depth, the temperature at 10 cm in the chambered plot was equivalent to surface temperature in the control plot (Table 3). No differences in soil moisture were detected between warmed and control plots at the time of sampling (Table 2a). However, continuous soil moisture data from the Lake Hoare site indicates that natural summer moisture inputs to warmed plots are amplified, either from collecting snow or from melting of subsurface ice (Table 3). While soil moisture at the time of sampling was not affected by experimental warming, geographic and inter-annual variation were significant, most noticeably at the Lake Bonney site after 2001/2002, following an unusually warm period (Tables 1 and 2a; Fig. 1a).

The effect of experimental warming on electrical conductivity (EC), a measure of soil salinity, varied among basins, but salinity was generally higher in plots with chambers (P < 0.01; Fig. 2). Overall, soils from the Lake Hoare site exhibited the lowest EC compared to other basins. Soil pH was influenced by moisture additions, year, and site (Table 2a). Overall, soil pH was highest at Hoare, and lowest at Bonney (Fig. 1b). Soil pH increased in plots that received moisture additions in 2001/2002 at Bonney (P < 0.01) and 1999/2000 at Fryxell (P < 0.01). All basins experienced inter-annual variation in pH over the course of the experiment (Fig. 1b).

The response of soil surface chlorophyll *a* concentration to experimental warming was variable across basins and not affected by experimental moisture additions. Chlorophyll *a* concentrations in warmed plots decreased at Bonney (P < 0.01) and increased at Fryxell (P = 0.03) in 2002/2003. After eight years, chlorophyll *a* concentrations increased in all plots at Bonney (P < 0.01) while remaining very low at Fryxell and Hoare (Fig. 1c). No data are available for the 2004/2005 austral summer for Bonney.

3.2. Population dynamics

Nematode communities were dominated by *S. lindsayae*, which accounted for 97–99% of animals in the plots, regardless of treatment. *Eudorylaimus* spp was the second most abundant nematode

Table 2

F-values of repeated measures ANOVA on the effect of basin, treatment (increased temperature, increased moisture), time of sampling, and interaction effects on (a) soil characteristics and (b) species abundance. *P < 0.05, **P < 0.01, ***P < 0.001.

(a)							
Effect	Soil moi	sture	pН		Chlo	rophyll a	EC
Basin	96.61***		136.87**	*	43.65		31.70***
Year	46.79***		75.52**	*	15.03	8***	31.73***
Temperature	1.23		0.03		16.08	3***	10.49**
Moisture	0.01		6.30**	ŧ	0.0	1	1.65
$Temp \times moist$	0.14		0.93		4.87		0.27
Basin × year	58.38***		37.34***		27.05***		6.06***
Basin × temp	0.87		1.62	43.20		5***	9.44***
$Basin \times moist$	0.01		1.59		0.10	5	1.16
Year × moist	0.34		1.77		0.75	5	1.36
Year \times temp	2.88		1.03	11.02		2***	4.53**
(b)							
	Nematodes						
Effect	S. lindsayae	Eudorylair	nus spp	P. mu	rrayi	Rotifers	Tardigrades
Basin	140.46***	165.69***		3.31*		50.19***	26.26***
Year	38.00***	26.97***		0.48		8.34***	6.00***
Temperature	20.17***	12.41***		1.89		16.91***	2.98
Moisture	0.31	1.03		0.18		0.52	0.11
$Temp \times moist$	0.55	0.01		0.56		0.82	0.06
Basin × year	3.91***	7.75***		1.10		4.21***	2.92**
$Basin \times temp$	0.33	0.21		0.56		3.54*	1.31
Basin imes moist	0.08	0.10		0.04		0.05	0.09
Year \times moist	0.61	0.15		1.81		0.55	0.50
Year \times temp	9.23***	9.84***		0.56		1.58	3.37**

Table 3

Austral summer soil temperatures (°C) and moistures (% g/g) inside and outside an ITEX chamber at three depths. Data were collected using thermocouples and theta probes on the south side of Lake Hoare and reflect post-processed daily running means averaged (±standard error) from December 1, 1999 to February 28, 2005.

Month	Depth (cm)	Temperature	(°C)	Soil moisture (% g/g)	
		Control	ITEX	Control	ITEX
December	0	6.02 (0.24)	8.66 (0.26)	1.44 (0.11)	2.62 (0.08)
	5	4.63 (0.20)	6.38 (0.23)		
	10	3.98 (0.19)	5.28 (0.20)		
January	0	4.80 (0.26)	7.52 (0.25)	2.50 (0.13)	2.99 (0.09)
	5	3.98 (0.21)	5.91 (0.20)		
	10	3.74 (1.9)	5.30 (0.17)		
February	0	-4.14 (0.33)	-1.47 (0.33)	2.45 (0.19)	2.92 (0.10)
	5	-3.82 (0.21)	-1.92 (0.30)		
	10	-3.74 (0.19)	-1.66 (0.29)		

making up between 0.2% and 3% of the community. *Plectus murrayi* were the least abundant nematodes and accounted for less than 0.1% of the nematode community. Rotifers and tardigrades were absent from most samples, but when present were higher in overall density than *P. murrayi*, constituting between 0.01% and 0.6% of the soil biotic community, respectively.

Nematode populations were strongly affected by warming treatments (Table 2b), but not by moisture treatments. After eight years of treatment, abundance of live *S. lindsayae* and *Eudorylaimus* spp was lower in plots subjected to experimental warming compared to control plots (P = 0.03 and P = 0.04 respectively) in two out of the three basins. Rotifer populations were also negatively affected by the warming treatment (P = 0.05). Populations of *P. murrayi* in warmed plots did not differ from controls (P = 0.16).

In addition to being negatively affected by experimental warming, population densities of the two most abundant nematode species varied over time, and among basins (Figs. 3 and 4; Table 2b). At Bonney, S. lindsayae declined in both ambient (P < 0.01) and warmed plots (P < 0.01) between 1999 and 2003 and continued to decline in warmed plots until 2004/2005. Populations of S. lindsayae at Hoare exhibited inter-annual variability with no directional trend (Fig. 3b). At Fryxell, S. lindsayae decreased in all years in all plots, but declines were most pronounced in the warmed plots (Fig. 3c). Populations of Eudorylaimus spp at Bonney peaked in 2002/2003 and 2006/2007 (Fig. 4a). At Hoare, no Eudorylaimus spp were recovered from plots with warming chambers (Fig. 4b). Overall, very few Eudorylaimus spp (0-30 viable individuals per kilogram dry soil) were found at Hoare, and the populations were much lower than those in the other basins. Eudorylaimus spp populations at Fryxell have remained relatively stable (Fig. 4c).

3.3. Species traits

Average body size of individual adult *S. lindsayae* was negatively affected by increased temperature (P < 0.01), and nematodes were smaller in warmed plots at Fryxell and Hoare compared to Bonney. Individual biomass decreased over time as well; on average, nematodes were smaller in 2004 compared to those collected in 1999 (P < 0.01). While individual nematodes tend to be smallest at Fryxell and increase in size toward Hoare and Bonney, this trend was only significant in 1999 (P < 0.01). Population biomass was highest at Fryxell for both years (P < 0.01).

There were no differences in sex ratio (the number of males per female) for *S. lindsayae* among treatments, but the number of males to females decreased (P = 0.029) at Bonney in 2002/2003 (Fig. 5a). The ratio of living juveniles to living females was highest at Fryxell and lowest at Hoare, and decreased (P < 0.01) over the course of the experiment (Fig. 5b). Mortality (number of live to dead nematodes) in *S. lindsayae* was highest at Bonney in 2002/2003 (P < 0.01) (Fig. 5c).



Fig. 1. Soil characteristics (mean \pm S.E.) (a) Gravimetric soil moisture (% g/g soil); (b) Soil pH; (c) Chlorophyll *a* concentrations (μ g/g soil), over eight years in three basins in Taylor Valley. Gray shaded box represents the flood event at Bonney. Because there were no differences between treatments, values were pooled for each basin (n = 12).



Fig. 2. The effect of increased temperature treatments on electrical conductivity (mean \pm S.E.) in (a) Bonney; (b) Hoare; and (c) Fryxell basins. Dashed lines represent elevated temperature treatments. Note that the scales are inconsistent due to large differences in natural salinity levels among basins. Gray shaded box represents the flood event.

4. Discussion

We simulated climate change by experimentally increasing temperature and moisture inputs to Taylor Valley soils for eight years. We also had the opportunity to study a natural warming event that flooded the experimental site in the westernmost lake



Fig. 3. The effect of increased temperature treatments on mean abundance (\pm S.E.) of *Scottnema lindsquae* over eight years in three basins in Taylor Valley. Dashed lines represent elevated temperature treatments Note that the scales are inconsistent due to large differences in natural populations among basins. Gray shaded box represents the flood event.

basin (Bonney). Because of inherent differences in the environmental constraints at each site (e.g., temperature, pH, salinity, nutrient limitations, parent material, topography), we predicted that biotic populations would respond differently to environmental change (Parsons et al., 2004). However, individual species responded to both the long-term experimental warming and the flood event in a consistent manner that fits our current knowledge of their physiological tolerances and habitat preferences.



Fig. 4. The effect of increased temperature treatments on mean abundance (\pm S.E.) of *Eudorylaimus* spp over eight years in three basins in Taylor Valley. Dashed lines represent elevated temperature treatments Note that the scales are inconsistent due to large differences in natural populations among basins. Gray shaded box represents flood event.

Our data show that *S. lindsayae*, the most abundant and widely distributed nematode in the McMurdo Dry Valleys (Freckman and Virginia, 1997; Powers et al., 1998; Wall, 2005), was sensitive to the warming treatment; populations of this nematode were 42% lower in warmed compared with control plots over the course of this experiment. Sensitivity to environmental change is not uncommon

Bonney

Hoare

Fryxell

Fig. 5. Life cycle parameters (mean \pm S.E.) for *S. lindsayae* (a) Sex ratio, or number of living males per living female; (b) number of living juveniles per living female; (c) Mortality, or number of dead nematodes per living nematode. Gray shaded box represents flood event at Bonney.

2004/2005

2005/2006

2006/2007

among many nematode species, and the temperature range that a particular species may tolerate can be narrow, which will often determine their distribution (Nicholas, 1984; Ferris et al., 1995). Changes in nematode abundance and community structure have recently been linked to both regional climate cooling (Doran et al., 2002b), and to a recent discrete summer warming event (Barrett et al., 2008b). Long-term climate and soil data from experimental sites at Lake Hoare pointed to a strong negative relationship between cooler summer temperatures and populations of S. lindsayae, which decreased by 10% per year from 1993 to 2005 (Doran et al., 2002b; Barrett et al., 2008a). Barrett et al. (2008a) later reported that record high temperatures in the austral summer of 2001-2002 did not slow or reverse a long-term decline in populations of S. lindsayae between 1993 and 2005 across Taylor Valley. Furthermore, the increase in available soil water associated with the warming event was correlated with a valley-wide increase in the algal-feeding Eudorylaimus spp between 2001 and 2005, especially at Lake Bonney, where previously dry soils remained moist for several years after the flood (Barrett et al., 2008a). Although the changes in nematode abundance attributed to climate warming in the current experiment occurred over relatively short temporal scales, it is reasonable to expect that expansions and contractions of nematode populations and ranges would be expected if these favorable conditions become more continuous under climate change.

More specifically, inter-annual variation in soil moisture, caused by natural climate variation (Barrett et al., 2008b) and by the presence of the warming chambers, contributed significantly to nematode population dynamics. The warming event of 2001-2002 resulted in record stream discharge, increased lake levels and melting of ground ice in some locations (Foreman et al., 2004; Lyons et al., 2005; Doran et al., 2008). The magnitude of this natural pulse to the system is evident in the significant rise in lake levels (0.56-0.70 m) across Taylor Valley between December 2001 and January 2002 (Barrett et al., 2008a; Doran et al., 2008). At Bonney, our experimental plots were flooded shortly after sampling in 2001-2002 (Lyons et al., 2005; Harris et al., 2007). This prolonged saturation coincided with an increase in chlorophyll a (and presumably microalgal biomass) in our plots in 2002–2003. Flooding also contributed to changes in water geochemistry (Lyons et al., 2005). This may have caused the initial decrease in electrical conductivity and pH of the soil after 2001–2002, presumably by dilution from low conductivity melt water, and eventually a spike in conductivity in 2004 that coincided with a decrease in soil moisture and a concentration of salts 3 years after the flood. Lyons et al. (2005) suggested that salts mobilized by seeps are transported to the surface soil by evapo-concentration. Similar dynamics are evident on the margins of dry valley lakes and streams were wicking of water contributes to spatial patterns in soil salinity and solute composition (Northcott et al., 2009). This suggests that events such as soil flooding can contribute to both the dilution and redistribution of salts in dry valleys soils. Hence, infrequent flooding may have both positive and negative effects on nematode populations as well as their food sources, considering the strong influence of salinity on their physiology and distribution (Nkem et al., 2006; Poage et al., 2008). This effect could be magnified by the presence of the chambers, which stress the system through changes in temperature and evaporation.

Distribution and abundance of *S. lindsayae* is highest in dry soil, and decreases significantly with proximity to streams and lakes (Treonis et al., 1999; Ayres et al., 2007). Therefore, it is not surprising that densities of live individuals at Bonney decreased in the years following the flood and have only recently begun to recover. These polar soils lack the functional redundancy seen in the invertebrate communities of temperate soils; thus the loss of the dominant nematode could have a substantial impact on food web dynamics and ecosystem functioning (Wall, 2007; Barrett et al., 2008b). In dry soils, *S. lindsayae* often occurs as the sole invertebrate (Wall and Virginia, 1999). Even near aquatic-terrestrial interfaces, where

increased soil moisture favors other species, *S. lindsayae* can make up a large portion of the nematode community, especially in sediments high in evaporated salts (Treonis et al., 2005). Using a ¹³C tracer added to soils in Taylor Valley, Barrett et al. (2008b) determined that the nematode community (overwhelmingly dominated by *S. lindsayae*) accounted for a disproportionate fraction of the heterotrophic C flux despite their small biomass, and that their influence was non-additive and species-specific. Barrett et al. (2008b) estimate that the 65% decline in *S. lindsayae* in Taylor Valley from 1993 to 2005 contributes to a 32% loss of function in C cycling.

Unlike *S. lindsayae, Eudorylaimus* spp, an omnivore/algal feeder, generally prefers moist to saturated soils with abundant algae or moss, because it relies on contemporary sources of organic matter (Wall, 2007). The unusual warming event that triggered flooding at Bonney created environmental conditions that favor *Eudorylamius* spp, which has been positively correlated with soil moisture and chlorophyll *a* (Courtright et al., 2001; Barrett et al., 2008a). High concentrations of chlorophyll *a* in all plots at Bonney suggest increased soil algae compared to Fryxell, where *Eudorylaimus* spp were less abundant in the warmed plots. Therefore, *Eudorylaimus* spp benefited from the increase in moisture at Bonney during the flood year (Barrett et al., 2008a) which may have overly compensated for the negative effect of increased temperature caused by the experiment itself.

Despite an increase in chlorophyll *a* at the Lake Bonney site after the flood, Eudorylaimus spp declined sharply in 2004/2005, coinciding with an increase in conductivity and a decrease in moisture. This suggests that direct effects of warming on Antarctic soil communities interact with changes in water activity (Hunt et al., 2007) and surface geochemistry, affecting food sources and local soil chemistry through the redistribution of salts. Evidence from the Lake Hoare site (Table 3) suggests that the presence of the warming chamber itself may change soil water availability throughout the season with implications for concentration of salts in surface soils. Salinity was typically higher in chambered plots, where a more pronounced wet/dry cycle may have amplified the movement of salts (e.g., Gooseff et al., 2007), as is common in stream and lake margins where frequent wetting and drying results in high sediment salt concentrations (Northcott et al., 2009). This may be an important indirect effect of increased temperature. S. lindsayae tolerates higher levels of salinity than either Eudorylaimus spp or P. murrayi (Nkem et al., 2006) and therefore can survive in dry, salty soils where the others cannot. However, there is a limit to this ability; above a salinity threshold of 1000 µS/cm the distribution of S. lindsayae is also negatively affected (Poage et al., 2008).

The lack of response to the experimental moisture additions was not expected, and may be the result of timing of inputs and the effects of course-textured soils on water retention (e.g. Hunt et al., 2007). In hot deserts with biological crusts or vegetation, the frequency and magnitude of pulse events create distinct reactions from soil biota (Whitford et al., 1981; Freckman et al., 1987) and even small events trigger a response from microbes (Austin et al., 2004). Unlike hot deserts, the dry soils of Taylor Valley are generally free of biological crusts, and low temperatures prevent the application of water until late summer when water could infiltrate into the thawed portion of the soil profile. Plots were intentionally sampled a full year after the moisture treatment was applied and therefore, this strategy did not allow for investigation of an immediate or brief response by the soil biota. We know that even small changes in soil moisture can have appreciable effects on soil water availability (Hunt et al., 2007), but the effect of our experimental moisture addition appears to be transient in these sandy soils (Ball et al., 2009). However, if a moderate annual pulse does not increase soil moisture for sufficient periods of time to alter the reproduction of Antarctic soil invertebrates, results from flooded plots at Lake Bonney show a clear response to a massive change in local hydrology. This one-time, natural pulse of melt-water increased soil moisture across Taylor Valley, detrimentally affecting populations of *S. lindsayae* while leading to an increase in numbers of *Eudorylaimus* spp, resulting in a significant biological response that persisted for several years (Barrett et al., 2008a).

Additionally, our climate data suggest that plots with chambers experience increased moisture throughout the season by trapping snowfall that provided increased moisture for algal growth. This effect may have been masked at Bonney due to the flooding, but at Fryxell and Hoare, chlorophyll *a* was higher in chambered compared to control plots, although this result was not significant (data not shown).

5. Conclusions

Our data show an overall negative effect of eight years of climate manipulations on nematode populations across Taylor Valley, which may have repercussions on community food web interactions and nutrient cycling. While experimental moisture additions did not appear to directly influence the biota in our study, a flood event had a noticeable negative effect on populations of S. lindsayae and a positive effect on Eudorylaimus spp. This flood allowed us to monitor a population change in conjunction with a natural climatic event, rather than an experimental one. Climate warming in Antarctica may increase soil moisture due to melting of snow packs, ground ice, and glaciers, (Foreman et al., 2004; Wall, 2007; Barrett et al., 2008b). Therefore, should the soils of the McMurdo Dry Valleys warm and/or become increasingly moist, our data show that populations of S. lindsayae, the most abundant and widely distributed animal in the dry valley region, may decrease, and habitat previously dominated by this species may become more suitable for other species. Because of the low diversity in this system, a substantial change in the relative abundance of a single species could disproportionately impact ecosystem functioning (e.g. carbon cycling) (Wall, 2007; Barrett et al., 2008b).

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