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Persistent effects of a discrete warming event on a polar desert ecosystem

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Abstract

A discrete warming event (December 21, 2001–January 12, 2002) in the McMurdo Dry Valleys, Antarctica, enhanced glacier melt, stream flow, and melting of permafrost. Effects of this warming included a rapid rise in lake levels and widespread increases in soil water availability resulting from melting of subsurface ice. These increases in liquid water offset hydrologic responses to a cooling trend experienced over the previous decade and altered ecosystem properties in both aquatic and terrestrial ecosystems. Here, we present hydrological and meteorological data from the McMurdo Dry Valleys Long Term Ecological Research project to examine the influence of a discrete climate event (warming of $>2\,^{\circ}$C) on terrestrial environments and soil biotic communities. Increases in soil moisture following this event stimulated populations of a subordinate soil invertebrate species (*Eudorylaimus antarcticus*, Nematoda). The pulse of melt-water had significant influences on Taylor Valley ecosystems that persisted for several years, and illustrates that the importance of discrete climate events, long recognized in hot deserts, are also significant drivers of soil and aquatic ecosystems in polar deserts. Thus, predictions of Antarctic ecosystem responses to climate change which focus on linear temperature trends may miss the potentially significant influence of infrequent climate events on hydrology and linked ecological processes.

Keywords: Antarctic dry valleys, climate change, extreme climate event, nematodes

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Introduction

Recent examples of extreme climate such as the European summer heat wave of 2003 and the devastating Gulf Coast hurricanes of 2005 have increased the recognition of discrete climate events as important controls over the structure and functioning of natural and managed ecosystems (Shar *et al*., 2004; Travis, 2005; Jentsch *et al*., 2007). Such events can be distinguished from directional climate trends (e.g. regional warming or cooling) on the basis of their frequency or likelihood of occurrence (Shar *et al*., 2004), and by the observed magnitude of consequences relative to the duration of the event (Jentsch *et al*., 2007). For example, timing and magnitude of precipitation and/or drought events in a variety of ecosystems exert strong influences over phenology, inter-specific competition, nutrient cycling, and primary productivity (BrassiriRad *et al*., 1999; Knapp *et al*., 2002; Austin *et al*., 2004; Jentsch *et al*., 2007). Although more attention has been focused on examples of directional climate trends that occur over sustained durations of time (e.g. regional warming), discrete climate events can have a disproportional influence over ecosystems relative to the temporal scales over which they occur.

Responses of ecosystems to both climate trends and events are current focuses of ecological research, particularly in dry environments (Peters, 2000; Schwinning & Ehleringer, 2001; McKay *et al*., 2003; Austin *et al*., 2004; Reynolds *et al*., 2004), where the importance of discrete climate events, traditionally described as pulses, has long been noted (Noy-Meir, 1973; Stafford

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Smith & Morton, 1990; Steinberger & Sarig, 1993; Gebauer & Ehleringer, 2000). In this context, discrete climate events can be extreme in terms of magnitude (e.g. intense precipitation events), but may not necessarily have negative impacts on the ecosystem. In fact, temporal climate variability and the importance of discrete precipitation events are characteristic properties of arid environments, which contribute to both the structure (i.e. community composition) and functioning (e.g. production) of desert ecosystems. This sensitivity to discrete climate events may also apply to polar deserts (Robinson *et al.*, 1998; Convey *et al.*, 2003). For example, pulses of liquid water following melt have been observed to rapidly reactivate freeze-dried microbial mats in stream channels (McKnight *et al.*, 2007) and contribute to nutrient loading in adjacent lacustrine ecosystems of the McMurdo Dry Valleys, Antarctica (Foreman *et al.*, 2004).

The McMurdo Dry Valleys (77°30′S, 163°00′E) are an ice-free environment in Southern Victoria Land Antarctica, where the National Science Foundation maintains a Long Term Ecological Research (LTER) project as a polar desert end-member among a network of sites studying the effects of inter-annual climate variability on aquatic and terrestrial ecosystems. The McMurdo Dry Valleys are near the environmental limits for the assembly of complex communities where multitrophic food webs of microbes and invertebrates occur (Laybourn-Parry *et al.*, 1997; Adams *et al.*, 2006; Barrett *et al.*, 2006). Thus, the dry valleys provide an excellent setting to examine the influence of climate trends and climate events on ecosystem structure and functioning because of the availability of long-term meteorological records and the extreme sensitivity of polar environments to climate variability (Chapman & Walsh, 1993; Fountain *et al.*, 1999).

The organisms comprising polar desert communities are well adapted to cold and dry conditions (Freckman & Virginia, 1997; Convey *et al.*, 2003). For example, soil nematodes, the most abundant and widely distributed metazoan taxa in the dry valleys, undergo anhydrobiosis to survive periods of extreme cold and/or aridity (Treonis *et al.*, 2000). Anhydrobiosis is a survival strategy induced by desiccation where organisms enter a dry, metabolically inactive state (losing >95% of water content), as a protection against environmental stress (Crowe & Madin, 1975). In this polar desert ecosystem, long periods of inactivity appear to be an important aspect of nematode life history and their activity is likely restricted to periods following the availability of liquid water (Treonis *et al.*, 2000). However, it remains unknown how discrete changes in ambient temperature and pulses in the availability of liquid water might affect soil communities and linked ecosystem functioning in this polar desert environment. Here, we examine the effects of recent climate variability in the McMurdo Dry Valleys on terrestrial and aquatic ecosystems. We present climate and hydrological evidence of glacial and subsurface ice melt following a discrete warming event during the 2001–2002 Austral summer (Foreman *et al.*, 2004; Lyons *et al.*, 2005) and examine the response of soil communities to changes in soil water availability.

Methods

Study site

The McMurdo Dry Valleys are a series of generally east to west-oriented glacially carved valleys located between the Ross Sea and the Polar Plateau in Southern Victoria Land, Antarctica. Taylor Valley (Fig. 1) is the main focus of McMurdo LTER project and has the longest records of continuous meteorological observations (1986–present) among the dry valleys (Doran *et al.*, 2002a). Mean annual temperatures in Taylor Valley range from −30.0 to −14.8 °C, with 10–100 days when average daily temperatures exceed 0 °C (Fountain *et al.*, 1999; Doran *et al.*, 2002a). Average annual precipitation is less than 10 cm water equivalent (Fountain *et al.*, 1999; Witherow *et al.*, 2006). Precipitation events in the dry valleys occasionally cover the landscape with snow up to several centimeters, but most of this water is unavailable to soil organisms because of high sublimation rates (Chinn, 1993; Treonis *et al.*, 2000). During the summer, snow cover lasts for only a few hours to days before sublimating and partly melting into the subsurface soil (Campbell, 2003). In the winter, low temperatures prohibit melting and losses of snow occur as sublimation. Thus, winter snow influences local hydrology only when and where it accumulates into snow patches on the leeward side of hills and boulders and survives into the summer melt season. These snow patches can be up to 1 m deep and tens of m^2 in area depending on the topography and are a significant source of moisture to proximate soil communities (Gooseff *et al.*, 2003). Subsurface ice may also provide a source of water to soil communities during brief melt periods (Lyons *et al.*, 2005; Harris *et al.*, 2007), particularly those distant from snowpacks and aquatic environments.

Low elevation soils of Taylor Valley typically occur on poorly developed mid-Holocene to Pleistocene tills, composed of diorites, granites, and sandstone (Campbell & Claridge, 1987; Bockheim, 1997). Soils in this region are poorly weathered, typically with high pH and salt content (Campbell & Claridge, 1987) and exceptionally low moisture and organic matter

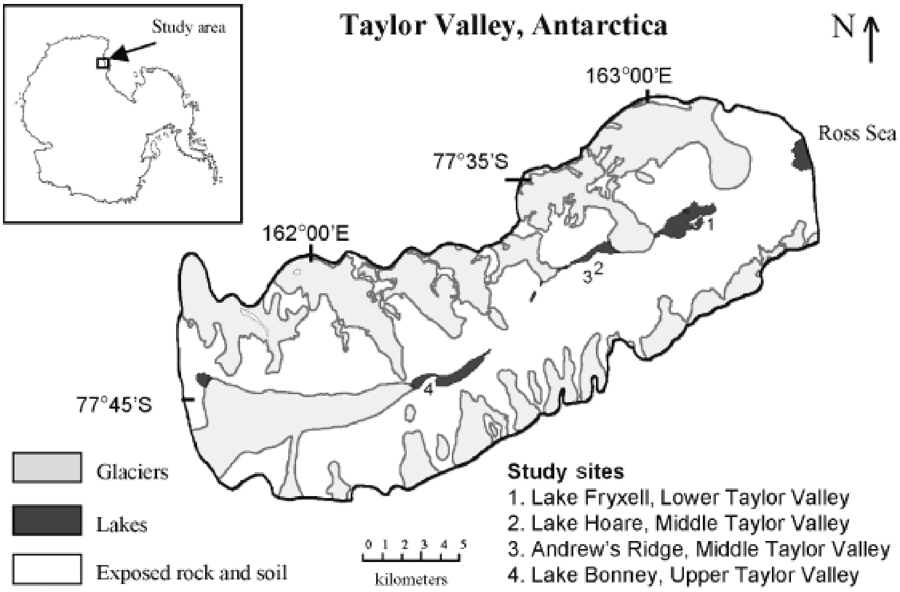

Fig. 1 Location of study sites in Taylor Valley, Antarctica.

availability (Barrett *et al*., 2004). Soils considered in this study are characterized by weak soil horizon development and shallow profiles with ice-cemented layers or dry permafrost occurring within 30–50 cm of the surface.

Soil communities of the dry valleys are composed of microorganisms (i.e. bacteria, fungi, and protists), and zero to four phyla of metazoan invertebrates (Adams *et al*., 2006). Nematodes are the most widely distributed and abundant metazoan, with four species identified in the dry valleys (Adams *et al*., 2006), although communities with more than two species are uncommon (Barrett *et al*., 2004). Of the nematode species found in the dry valleys, the microbivore *Scottnema lindsaye* Timm (1971) is the most abundant and widely distributed (Freckman & Virginia, 1997). *S. lindsayae* appears to be well adapted to the arid soils relative to the other metazoan invertebrates found in this region which are typically limited to intermittently wet soils and sediments near streams and lakes (Treonis *et al*., 1999; Ayres *et al*., 2007). Two subordinate species of nematode, *Eudorylaimus antarcticus* Yeates, 1970 and *Plectus antarcticus* de Man, 1904 Timm (1971), are typically present in lower numbers than *S. lindsayae* in dry soils (Barrett *et al*., 2004), but are more abundant in saturated environments in or adjacent to stream and lake sediments (Treonis *et al*., 1999; Barrett *et al*., 2006; Ayres *et al*., 2007). Several taxa of rotifers and tardigrades (~3 genera each) inhabiting wet soils and sediments of the dry valleys have been reported, although their taxonomy remains largely unresolved (Adams *et al*., 2006).

We present a multiple-year record from control plots of ongoing soil experiments maintained by the McMurdo LTER (Table 1). These experiments are located at a series of sites in Taylor Valley which represent a range of physical conditions from most suitable to least suitable for soil invertebrate biota: lower Taylor Valley on the south side of the Lake Fryxell; two sites in middle Taylor Valley, one adjacent to the south side of Lake Hoare and one below Andrew's Ridge; and one study site located in upper Taylor Valley, south of the west lobe of Lake Bonney between the Bonney Riegel and the Taylor Glacier (Fig. 1).

Soil microclimate monitoring

Soil temperature and moisture data were collected adjacent to a long-term (1993–2005) experiment on the south side of Lake Hoare in middle Taylor Valley. Soil temperature has been continuously monitored since 1995 using a Campbell CR10XT data-logger (Campbell Corporation, Logan, UT, USA) and thermocouples buried at three depths (surface, 5 cm, and 10 cm depths). Soil temperatures are read every 30 s, averaged, and stored at 10-min intervals. Soil water content was estimated at 5 cm depths with soil reflectometry using Theta Probe ML2 (Delta-T Devices, Cambridge, UK). Soil reflectometry measurements were logged daily starting in December 1998, and soil water contents are presented when temperatures permit liquid water. The theta probes were calibrated with known volumetric moisture contents of soils collected from the Lake Hoare site. Estimates of gravimetric soil moisture (% g/g)

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Table 1 Location of soil study sites in Taylor Valley, Antarctica

Study site	Latitude (°)	Longitude (°)	Elevation (m)	Duration of study
Lower Taylor Valley	77.608	163.247	20	1999–ongoing
Middle Taylor Valley (Lake Hoare)	77.633	162.882	90	1993–2005
Middle Taylor Valley (Andrew's Ridge)	77.635	162.877	101	1999–ongoing
Upper Taylor Valley	77.725	162.312	110	1999–ongoing

were calculated from the voltage output (v) of the theta probes using the following equation:

$$\phi = \left(\frac{1}{d}\right)(-251v^5 + 261v^4 - 101v^3 + 17v^2 - 1.05v) \times 100, \qquad (1)$$

where d is the bulk density of soils from the Lake Hoare study site ($1.6\,\mathrm{g\,mL^{-1}}$) and ϕ is the gravimetric soil water content.

Lake hydrology and geochemistry

Long-term measurements of lake hydrology (1972–2006) and geochemistry (1993–2006) are presented to provide an integrative assessment of regional climate conditions influencing Taylor Valley over the period of study. Early and late summer water-level measurements were made at Lakes Fryxell, Hoare and Bonney. Lake levels (measured on liquid water in drill holes or in lake moats) were optically surveyed relative to a USGS benchmark and expressed as meters above the 1972 lake levels when routine annual measurements began. Additional lake-level data from 1903, 1963, and 1964 reported by Chinn (1993) are plotted for Lake Bonney to extend insights through the 20th century. Chloride concentrations of Lake Hoare waters were measured on samples collected from various depths in Niskin bottles during the early part of the Austral summer before stream flow. Hundred milliliter aliquots were filtered through 0.4 µm nucleopore filters and analyzed for $\mathrm{Cl^-}$ on a DX-300 ion chromatographic system (Dionex, Sunnyvalle, CA, USA), as described by Welch *et al.* (1996).

Soil biology and biochemistry

Soil samples were collected from the top 10 cm of the soil profile with sterilized plastic trowels in December or January between 1993 and 2005 at the long-term study site on the south side of Lake Hoare ($n = 8$ sample collections of eight replicate samples), and from 1999 to 2005 at the study sites in lower, middle, and upper Taylor Valley ($n = 4$ sample collections of six replicate samples). An additional sample collection was made at the Bonney Riegel study site in upper Taylor Valley where a warming event in January 2002 resulted in flooded soil plots (Lyons *et al.*, 2005; Harris *et al.*, 2007). Soil samples were transported to the Crary Laboratory at McMurdo Station for analyses of soil biota. Soil metazoan invertebrates (nematodes, tardigrades, and rotifers) were extracted within 48 h of sample collection using a modified sugar-centrifugation extraction technique and identified and enumerated under light microscopy (Freckman & Virginia, 1997).

Water content of soil samples was determined from mass loss of soils heated at 105 °C for 48 h; physicochemical soil properties (pH, electrical conductivity) were determined using standard electrode techniques. Soil carbon and nitrogen content was measured with a Carlo Erba 1500 (CE Elantech, Lakewood, NJ, USA) on finely ground soils to determine total C and N, and on finely ground acidified soils to determine organic C (Barrett *et al.*, 2004). Chlorophyll *a*, an index of standing alga biomass (Roser *et al.*, 1993), was estimated for surface soils (0–2 cm) using an acetone extraction/flourometric procedure described by Barrett *et al.* (2004).

Statistical comparisons of nematode communities were made on $\log(X + 1)$-transformed estimates of total living nematodes to satisfy assumptions of normality. Population structure (dead/live, sex, proportion of juveniles) of nematode species was determined as reported by Barrett *et al.* (2004). Regression and analysis of variance (ANOVA) tests on soil biological and biochemical variables were performed in JMP for estimation of variance components explained by soil factors (SAS, Cary, NC, USA). Soil biota data are presented for all years while data representing chemical variables (C, N, pH, and conductivity) are based upon samples collected in the initial years of the study. Chlorophyll *a* content was estimated during each sample collection and used in statistical models evaluating controls over nematode populations; chlorophyll *a* data from the 2004–2005 summer season were used for comparisons among sites because these data had the fewest instances of samples with concentrations below detection limits.

Results

Climate

A discrete warming event occurred in the McMurdo Dry Valleys from December 21, 2001, to January 12,

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2002, when daily average temperatures exceeded the 10-year mean by more than 2 °C (Fig. 2a). Daily mean soil temperatures (averaged over 0–10 cm depth) ranged by more than 50 °C over the entire 10-year annual records, with winter minimums of −45 °C and summer maximum daily temperatures of 15 °C. The 10-year mean (±SD) summer (DJF) soil temperature at the Lake Hoare study site was 1.6 (±1.3) °C, with an average of 65 degree days above 0 °C per year for the period 1995–2005. Mean daily summer soil temperatures decreased significantly between 1995 and 2001 (Fig. 2a). The regression for this trend is as follows: soil temperature = 3.0−0.5 °C yr^{-1}, $P = 0.04$, $r^2 = 0.59$. This period was followed by a summer with above-average temperature (Fig. 2a), particularly during the first 2 weeks of January 2002. The 10-year mean (±SD) daily January soil temperature was 3.6 (±0.34) °C; the average daily temperature in January 2002 was 5.8 °C, exceeding the 99% confidence interval of this data record. These elevated temperatures coincided with a threefold increase in soil moisture (Fig. 2b).

Soil water content varied significantly among the study sites and over the course of the data collection. Mean gravimetric moisture content estimate from grab samples collected in soils at the Lake Hoare study site ranged by 2.1% (although variation among replicate samples occasionally exceeded this, indicating a high degree of spatial variation associated with soil water), with minimum levels of 0.37% in January 1995 and a maximum of 2.4% in December 1995 (Fig. 2b). Soil moisture estimates from theta probes had a larger range (4.3%) than grab samples, as expected from a record with greater temporal resolution (Fig. 2b). The lowest theta probe readings occurred between December 1999 and January 2000 when no grab sample data are available. Maximum values of soil moisture observed with theta probes occurred following the high temperatures of January 2002 (Fig. 2). High levels of soil moisture content persisted through the following 3 years. Similar temporal trends were evident from grab samples collected at the additional lower, middle, and upper Taylor Valley study sites, where gravimetric soil moisture was greatest in January 2002 (data not shown).

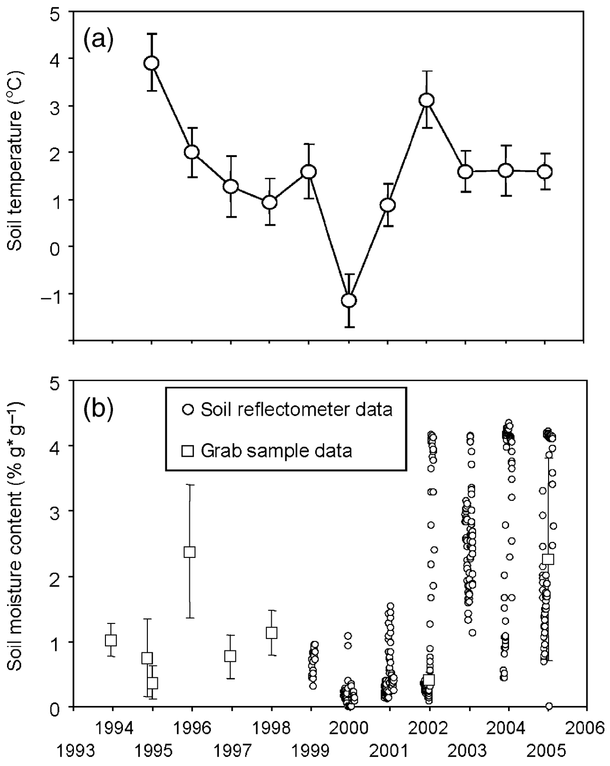

Fig. 2 Long-term temporal variation in surface soil (5 cm depth) temperature (a) and moisture content (b) at the Lake Hoare study site in middle Taylor Valley.

Lake hydrology and geochemistry

Taylor Valley lake levels increased by an average of 0.09 m yr^{-1} between 1972 and 2005, and three distinct phases of changes in lake levels are evident (Fig. 3). Continuous increases in lake levels were most pronounced between 1972 and 1991 when Lakes Hoare, Fryxell, and Bonney levels rose by an average of 0.09, 0.09, and 0.22 m yr^{-1}, respectively. In contrast, during the period of 1992 through November of 2001, lake levels dropped by 0.08, 0.05, and 0.04 m yr^{-1} in Lakes Fryxell, Hoare, and Bonney. Following this decade of lake-level decline, Taylor Valley lake levels increased again by 0.65, 0.56, and 0.70 m in Lake Fryxell, Hoare,

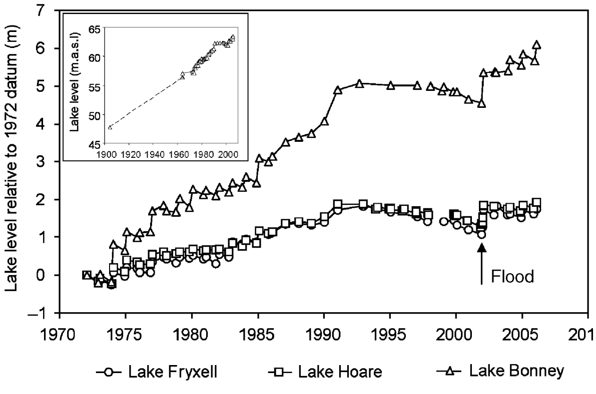

Fig. 3 Long-term trends in Taylor Valley lake levels relative to 1972 levels. The arrow indicates the timing of the flood event of January 2002. Inset shows updated data from Chinn (1993) illustrating an interpolated 103-year trend for Lake Bonney levels using data collected by R. F. Scott's *Discovery* expedition in 1903.

and Bonney, respectively, between December 2001 and January 2002, greatly exceeding previous observations of seasonal lake-level changes (Fig. 3).

Temporal variation in lake surface water geochemistry coincided with these changes in lake levels (Fig. 4). Lake Hoare Cl^- concentrations increased from 1993 to 2001 during a period of declining lake levels. These trends were followed by an abrupt threefold decrease in Cl^- concentrations in the mixolimnion in January 2002 (Fig. 4). This dilution of the mixolimnion resulted in increased stratification and stability of the water column. Changes in lake levels and solute concentrations were greatest in the first weeks of January 2002 when lake levels increased at rates of 3–8 m yr^{-1}, and Cl^- concentrations decreased by more than 50 mg L^{-1} (Fig. 5), coinciding with above-average summer temperature (Fig. 2a). These changes in lake hydrology and chemistry exceeded all other observations through the period of study (1972–2006 and 1993–2006 for lake levels and Cl^- concentrations, respectively).

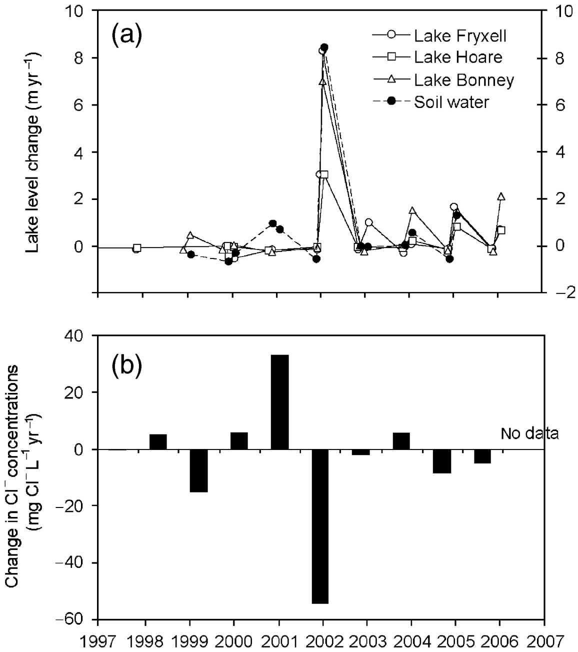

Fig. 5 Relative changes in lake levels, soil water content (a) and Lake Hoare Cl^- concentration (b) between 1997 and 2006.

Long-term soil-monitoring sites

Soil properties varied significantly among the sites in Taylor Valley (Table 2). Variation in soil organic matter content exhibited an east–west trend in Taylor Valley; soil organic C and total N content were greatest in soils near Lake Fryxell in lower Taylor Valley, followed by sites in middle Taylor Valley (Lake Hoare and Andrew's Ridge) and upper Taylor Valley (Table 2). Electrical conductivity (salinity) was greatest in soils from the Lake Bonney basin in upper Taylor Valley, followed by lower and middle Taylor Valley (Table 2). Soil chlorophyll *a* concentrations, low in all sites throughout the study (below detection to 0.5 mg kg^{-1}), were greatest in samples collected from upper Taylor Valley, particularly in January 2002 (Table 2).

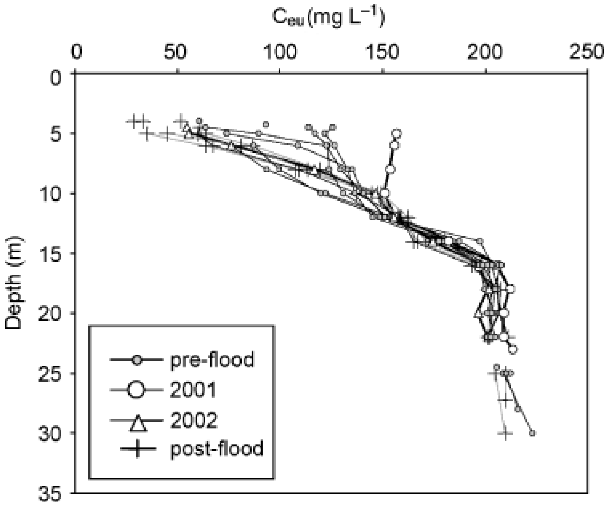

Fig. 4 Long-term trends in depth profiles of Cl^- concentrations in Lake Hoare.

These differences in soil properties contributed to spatial and temporal trends in nematode populations (Figs 6 and 7) and chlorophyll *a* concentrations, with 59% and 20% of the variance in populations of *S. lindsayae* and *E. antarcticus*, and 34% of the variance in chlorophyll *a* content accounted for by the main effect 'site' in an ANOVA model (Table 3). Soils from lower Taylor Valley had the largest populations of *S. lindsayae* and *E. antarcticus*, followed by soils from middle and upper Taylor Valley (Figs 6 and 7). No statistically significant variation in populations of *P. antarcticus* or in numbers of rotifers or tardigrades was detected; only low numbers of these organisms (<20 organisms kg soil^{-1}) were recovered from very few of the study plots.

Populations of the dominant soil organism, *S. lindsayae*, declined in all four monitoring sites (Fig. 6). Declines of *S. lindsayae* were most apparent in the lower and upper Taylor Valley sites following high temperatures and pulses of soil water in January 2002 (i.e. the 'flood', indicated by arrows in Fig. 6), when mortality increased by 14% ($P = 0.027$, two-tailed *t*-test). Temporal trends in *E. antarcticus* were also significant (Table 3), although unlike trends in *S. lindsayae* populations, they were not continuous or well represented by linear fits (Fig. 7). Populations of *E. antarcticus* peaked following the flood of January 2002, especially notable in upper

Table 2 Mean (±1 standard deviation) soil biogeochemical properties of study sites

Study site	Soil organic carbon (g kg^{-1})	Total soil nitrogen (g kg^{-1})	Chlorophyll *a* content (mg kg^{-1})	pH	Electrical conductivity (μS cm^{-1})
Lower Taylor Valley	$0.47^{a*} \pm 0.16$	$0.04^{a} \pm 0.01$	$0.017^{b} \pm 0.009$	9.4 ± 0.23	$153^{a,b} \pm 39$
Middle Taylor Valley (Lake Hoare)	$0.24^{b} \pm 0.06$	$0.04^{a} \pm 0.01$	$0.003^{c} \pm 0.001$	9.6 ± 0.25	$43^{c} \pm 13$
Middle Taylor Valley (Andrew's Ridge)	$0.18^{b} \pm 0.01$	$0.02^{b} \pm 0.01$	$0.005^{c} \pm 0.002$	9.8 ± 0.26	$95^{b,c} \pm 37$
Upper Taylor Valley	$0.17^{b} \pm 0.04$	$0.02^{b} \pm 0.01$	$0.23^{a} \pm 0.13$	9.7 ± 0.04	$200^{a} \pm 16$

*Means indicated by the same superscript letters are not statistically different ($P < 0.05$) by Tukey–Kramer comparison of means.

Taylor Valley when an additional sample collection was made immediately following this event (Fig. 7c). Increases in *E. antarcticus* were associated with changes in the number of juveniles present in the population; the proportion of juveniles making up *E. antarcticus* populations increased from an average of 54–71% following the flood. In general, *E. antarcticus* populations increased following pulses of soil moisture and chlorophyll *a* content. Soil water accounted for 22% of the variance in abundance of *E. antarcticus* across all sites. The untransformed regression parameters of *E. antarcticus* and soil water for all samples are as follows: *E. antarcticus* abundance = 1.6 × soil water + 15.1. Stronger fits between *E. antarcticus* and water are evident within specific sites (Fig. 8).

Discussion

One of the central axioms of polar science is that high-latitude ecosystems have heightened sensitivity to climate change (i.e. polar amplification), because of the strong influence of even minor variation in temperature on phase changes of water and its implications for hydrological and ecological responses (Chapman & Walsh, 1993; Fountain *et al.*, 1999). Perhaps, the strongest evidence of this sensitivity in polar regions is the significant loss of ice volume following regional warming in both the Arctic and Antarctic over the last 50 years (Anisimov *et al.*, 2007). Such changes in climate are expected to have profound consequences for both ecological and cultural systems in polar regions (Chapin *et al.*, 2005). However, sensitivity of polar ecosystems to climate change may also be exhibited following regional cooling trends. While the available instrumental record indicates that the Antarctic Peninsula has experienced significant warming over the past 50 years, other Antarctic regions have exhibited ambiguous climate trends, or even climate cooling (Vaughan *et al.*, 2003; Turner *et al.*, 2005; Anisimov *et al.*, 2007). For example, a recent summer cooling trend of 1.2 °C per decade in the McMurdo Dry Valley region of Antarctica resulted in significantly reduced glacial melt, increased lake-ice thickness, lower aquatic productivity, changes in diatom community composition, and a decline in soil invertebrate populations (Doran *et al.*, 2002b; Esposito *et al.*, 2006; Barrett *et al.*, 2008). Thus, polar ecosystems may exhibit sensitivity to directional climate change consisting of warming *or* cooling, because both types of climate trends influence the mass balance of ice vs. liquid water (Fountain *et al.*, 1999; Doran *et al.*, 2002b; Vaughan *et al.*, 2003).

Discrete climate events or experimental manipulations operating over seasonal time scales are also significant drivers of ecological structure and functioning in polar ecosystems (Scott & Rouse, 1995; Robinson *et al.*, 1998; Foreman *et al.*, 2004; Aerts *et al.*, 2006), although they have received less attention than directional climate change. These climate events could have persistent effects disproportional to the temporal scales over which they operate, such as occurs in other extreme environments. In temperate deserts, for example, short-duration climate events drive large changes in hydrology (Redmond & Koch, 1991; Ely, 1997), which in turn can structure persistent patterns of soil resources, vegetation and biota (Steinberger & Sarig, 1993; Gebauer & Ehleringer, 2000; Peters, 2000; Schwinning & Ehleringer, 2001; McKay *et al.*, 2003; Warren-Rhodes *et al.*, 2007). Polar desert ecosystems may be especially sensitive to discrete climate events considering the dual role that temperature and moisture play on the limitations over biological activity and movement of water. Our results indicate that discrete climate events can drive persistent changes in polar deserts of the McMurdo Dry Valleys and may have enduring effects disproportional to the temporal scales over which they operate as evidenced by the rapid increase in lake levels, reversing multi-year declines during a cooling trend.

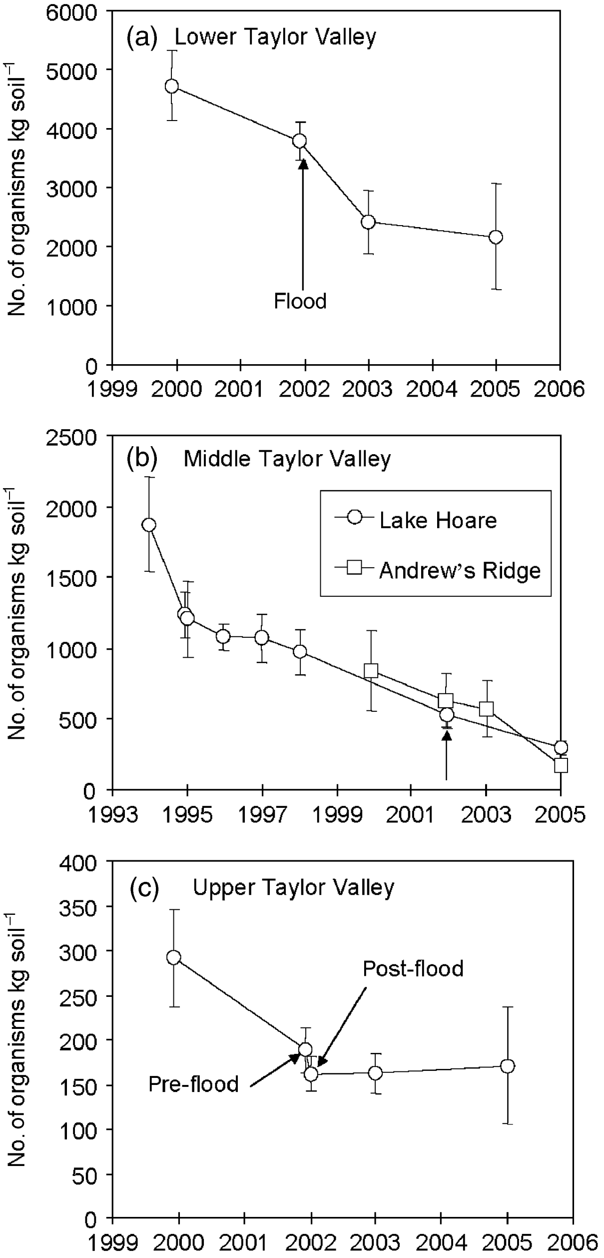

Fig. 6 Long-term trends in mean abundance (±1 standard error) of the Antarctic nematode *Scottnema lindsayae* at long-term study sites in lower (a), middle (b) and upper (c) Taylor Valley. The arrows indicate the timing of the flood event of January 2002.

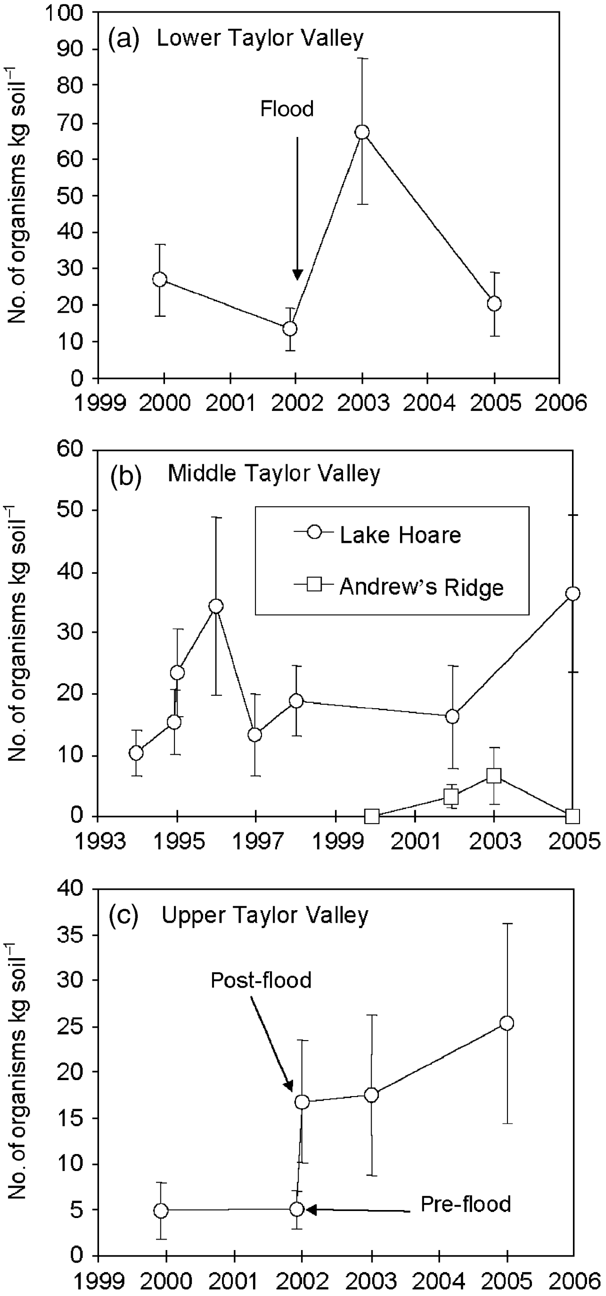

Fig. 7 Temporal variation in mean abundance (±1 standard error) of *Eudorylaimus antarcticus* at long-term study sites in lower (a), middle (b) and upper (c) Taylor Valley. The arrows indicate the timing of the flood event of January 2002.

Long-term climate trends

Closed-catchment lakes integrate basin-wide hydrology and geochemistry and are therefore useful indicators of regional climate conditions in both polar and temperate systems (Battarbee, 2000; Lyons *et al.*, 2000; Hodgson *et al.*, 2006). Lakes of the McMurdo Dry Valleys have unique hydrology and geochemistry due to perennial ice-cover and persistent stratification of waters that contribute to a rich paleo-climate sediment record (Doran *et al.*, 1999; Poreda *et al.*, 2004). Moreover, measurements of lake properties made during the initial exploration of the dry valleys by Robert Falcon Scott's *Discovery* expedition extend insights gained from measurements of lake levels made in the early years of the 20th century to the present (Chinn, 1993). The

Table 3 *F*-ratios from analysis of variance of soil nematodes, gravimetric water content and chlorophyll *a* concentrations by site and year

Source of variation	*S. lindsayae*	*E. antarcticus*	Soil water	Chlorophyll *a*
Site	61.76***	9.01**	7.87**	12.17***
Year	16.74**	3.2*	5.39*	12*

*$P<0.01$, **$P<0.001$, ***$P<0.0001$.

McMurdo Dry Valleys are useful model systems for examinations of climate because the observational and data records span periods of both warming and cooling conditions which contribute to variability in the mass balance of liquid water and ice that drive responses in hydrology and ecological processes (Foreman *et al.*, 2004; Fountain *et al.*, 2006; Doran *et al.*, 2008).

The results of Chinn (1993) and our data show that the dominant hydrologic trend through the 20th century has been a significant rise in Taylor Valley lake levels (Fig. 3, inset). These trends are strong indicators of increased glacial melt, presumably a result of regional warming from the early 20th century through the 1980s. Our records beginning in 1972 document a 19-year trend of increasing lake levels, followed by a period of relatively cold summers, low stream flow, and declining lake levels through the 1990s and early 2000s. This cooling trend ended abruptly during the Austral summer warming event of 2001–2002 when lake levels increased by almost a meter over a period of several weeks (Fig. 3). Such rapid changes in lake levels elicited significant changes in surface solute content, lake water stratification, aquatic primary productivity, and biogeochemical cycling, which have persisted over multiple years (Figs 3 and 4; Foreman *et al.*, 2004), even after a return to more moderate, average temperature conditions (Fig. 2a).

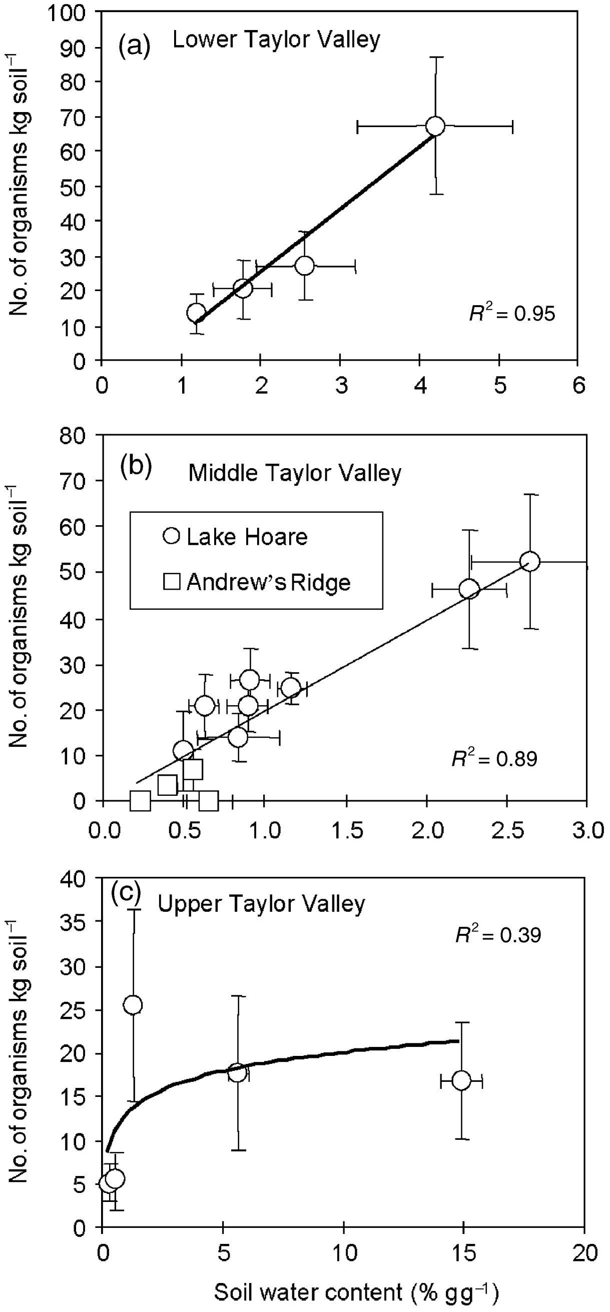

Fig. 8 *Eudorylaimus antarcticus* vs. soil water content in soils collected from long-term study sites in lower (a), middle (b) and upper (c) Taylor Valley (data points are means ±1 standard error).

Discrete climate events

The McMurdo Dry Valleys have experienced episodes of directional climate change (both warming and cooling) punctuated by discrete events on seasonal to annual scales that have profound influence on terrestrial and aquatic systems (Chinn, 1993; Doran *et al.*, 2002b; Nylen *et al.*, 2004; Doran *et al.*, 2008). The summer of 2001–2002 was the warmest summer on record since continuous monitoring of temperature began in 1985 (Doran *et al.*, 2002a). Record high temperatures between December 21, 2001, and January 12, 2002, were associated with strong katabatic winds that facilitated a period of rapid warming (Nylen *et al.*, 2004) and melting (Lyons *et al.*, 2005; Harris *et al.*, 2007), resulting in record stream discharge (Doran *et al.*, 2008), record increases in lake levels and soil moisture (Fig. 5), enhanced nutrient export to lakes (Foreman *et al.*, 2004), and a persistence of elevated water content in some soils across several years (Fig. 2b). The influence of the high-melt summer of 2001–2002 on lake biogeochemistry has been described by Foreman *et al.* (2004), the consequence of which was to increase nutrient export and primary production in the following years. In less than one summer season, lake levels increased by nearly 1 m, while it took over a decade for lake levels to decrease by a similar magnitude (Fig. 3). The changes in lake levels observed in January 2002 were the greatest of the 24-year record.

Temporal variation in lake water balance drives concurrent changes in surface water geochemistry of closed-basin lakes typical of the McMurdo Dry Valleys and other cold desert environments. In the dry valleys, the primary source of water to the lakes is dilute meltwaters flowing from the glaciers either through stream channels or from direct melting into lakes (Fountain *et al*., 1999). Liquid water is lost from the lakes by evaporation and sublimation of the ice covers and by freezing water onto the bottom of the ice covers during winter. As new ice is accreted onto the bottom of the ice covers, salts are exsolved from the ice matrix and the solute concentrations in the mixolimnion increase.

During low stream flow years, the water lost due to ablation of the ice covers is not balanced by new glacial melt-water and the solute concentrations in the mixolimnion increase relative to the previous year. For example, the surface water chloride concentrations in ice-covered Lake Hoare generally increased from 1993 to 2001 during a period of relatively cold summers and low stream flow. Following the flood year in the Austral summer of 2001–2002, solute concentrations in the upper water column decreased by approximately threefold to 1993 levels (Fig. 4). The observed variation in climate-driven hydrology caused large changes in the physical structure of the lake environment as well as significant differences in biogeochemical cycling and phytoplankton productivity (Foreman *et al*., 2004). Extreme climate events such as the high melt and nutrient discharge of 2001–2002 provide boundary conditions for hydrological and biogeochemical budgets and may have an enduring influence on aquatic ecosystems of the dry valleys. Warm years may also play a similarly crucial role in soils, where melting of ground-ice can create seeps and recharge water stored in surface soils where it is available to support biological activity in subsequent years (Lyons *et al*., 2005). Because distribution of these seeps is not uniform, these melt events may also contribute to the spatial heterogeneity of the soil environment.

Climate effects on soil ecosystems

Nematodes are the Earth's most abundant metazoan taxa and are nearly ubiquitous in soil environments as free-living organisms where they inhabit microscopic water films (Boag & Yeates, 1998; Ferris *et al*., 2001); thus, soil nematodes are useful indicators of the sensitivity of soil biological communities to environmental change. In contrast to other terrestrial environments, distribution of soil nematodes in the dry valleys is not ubiquitous. Nematodes are absent from more than 30% of the soil habitats examined and thus illustrate the limits for multicellular life in Antarctic soils (Freckman & Virginia, 1997). Distribution of these and other metazoan invertebrates varies markedly over environmental gradients structured by the amount of water, organic carbon, and soluble salts in the surface soil (Freckman & Virginia, 1997; Barrett *et al*., 2004; Poage *et al*., 2008). However, the responses of the most common invertebrates to these soil physicochemical parameters vary considerably among taxa and communities types (Treonis *et al*., 1999). Thus, more diverse soil communities may exhibit greater resilience to environmental change and increased activity and reproduction following sudden climatic events, such as occurred during the flood year.

Despite the increases in availability of soil water in January 2002, the dominant terrestrial organism, *S. lindsayae*, did not increase in abundance, and in fact continued a decadal population decline across several sites in Taylor Valley (Fig. 6). This pattern is consistent with previous reports of *S. lindsayae*'s apparent aversion to saturated soils (Treonis *et al*., 1999; Ayres *et al*., 2007). In contrast, inter-annual variability in the often co-occurring subordinate nematode species *E. antarcticus* was associated with observed pulses of soil moisture, particularly during January 2002 (Figs 7 and 8). *E. antarcticus* abundance and recruitment of juveniles increased following the pulse of soil moisture availability in all three lake basins of Taylor Valley. The linear fits between soil moisture and *E. antarcticus* numbers were generally discontinuous (Fig. 8), which suggests that such bimodal distributions of soil moisture may be typical features of dry valley soils.

The responses of individual soil nematode species to seasonal and inter-annual variability in soil moisture were similar in sign to previous descriptions of spatial correlations in soil communities with soil water (positive for *E. antarcticus*, negative for *S. lindsayae*), but were generally stronger (Treonis *et al*., 1999; Ayres *et al*., 2007). For example, Freckman & Virginia (1997) found that soil water content accounted for 15% of the variation in spatial distribution of *E. antarcticus* in a regional survey of the dry valleys (partial r^2 of 0.15 between abundance of *E. antarcticus* and soil water from a multiple regression model), while we found that temporal trends in soil water explained 39–95% of the variation in populations of *E. antarcticus* (Fig. 7). Thus, the temporal response of nematode populations to variation in soil moisture was greater than the response to variation in soil moisture encountered over spatial gradients. Similar contrasts in the response of ecosystems to temporal vs. spatial variability of physical drivers have been reported for semiarid grasslands and savannas, where primary production and nitrogen mineralization responses to inter-annual or geographic variability in precipitation are mediated by the resident communities (Lauenroth & Sala, 1992; O'Connor *et al*., 2001; Barrett *et al*., 2002). The greater response of nematode species to temporal moisture variability relative to variation over spatial gradients suggests that as in other dry ecosystems, the relatively short-term functional responses of an ecosystem to climate are constrained by the initial community structure.

Discrete climate events such as the warm, wet conditions of January 2002 may play a crucial role in the structure of soil communities and the physical properties of dry valley ecosystems. The carry-over effects of these rare to infrequent climate events on soil moisture and lake hydrology and chemistry can be large, erasing the accumulated ecosystem influences from longer term but less pronounced trends in climate variation. Melting of ground-ice in warm years or seasons can contribute to elevated water availability in surface soils for several years, despite a return to average or even cooler temperatures in subsequent summers (Fig. 2b). Lake-level data and stream flow records suggest that previous episodes of elevated summer temperatures and high-melt conditions may have also occurred in 1972, 1985, and 1991 (Chinn, 1993). Such pulses in moisture availability may be important to maintain soil biodiversity by facilitating the survival, reproduction, and growth of subordinate species with higher water requirements, indicating that far from being redundant species, these less common species provide resilience to environmental change. The general ability of these organisms to survive desiccation through anhydrobiosis following drying of the soils probably accounts for the weak spatial correlations between nematode diversity or biomass and soil moisture (Freckman & Virginia, 1997; Treonis *et al*., 2000), as the spatial distribution of soil organisms at any one time may be a legacy of previous soil moisture conditions controlled by climate trends and extreme events. Similar responses of biotic communities to moisture pulses have long been noted in dry temperate ecosystem deserts (Noy-Meir, 1973; Freckman *et al*., 1987; Reynolds *et al*., 2004).

These results illustrate the sensitivity of polar ecosystems in general to small changes in climate conditions, where abrupt climate events can illicit significant changes in hydrology and biogeochemical cycling. In the dry valleys, these pulses of resource availability may stimulate or maintain biodiversity by providing microclimate and physical conditions that allow subordinate species to grow and reproduce in advance of the return of more limiting environmental conditions. Predictions of Antarctic ecosystem responses to climate change that focus on linear warming trends may overlook the potentially significant influence of extreme or infrequent climate events on hydrology and linked ecological changes.

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