



Thawing permafrost alters nematode populations and soil habitat characteristics in an Antarctic polar desert ecosystem[☆]

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ABSTRACT

Spatial distribution of soil nematode populations in Antarctic terrestrial ecosystems is tightly controlled by environmental factors and thus highly sensitive to changes in soil properties. Increases in the magnitude and frequency of episodic warming events as well as eventual warming trends are likely to result in increased water availability due to glacial melting and permafrost thaw, and may also incite changes in soil physical and chemical characteristics that determine nematode habitat suitability. We hypothesized that climate warming would result in new suitable soil habitats leading to heightened diversity and activity in nematode communities. In order to test this hypothesis, we compared nematode populations in patches of soil wetted by naturally enhanced permafrost thaw versus adjacent soils unaffected by thaw. We found that thaw sites had significantly lower nematode abundances and living to dead ratios, contradicting our hypothesis. We also observed significantly altered soil texture (finer particle size), lower pH and higher salinity in permafrost seeps. These observations suggest that current and future changes in climate may alter soil properties and result in significant changes in nematode population structure, distribution and function.

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Introduction

High latitude ecosystems are projected to experience future rises in temperature, resulting in thawing glaciers and permafrost and thus increased available soil moisture (Chapin 2005). As liquid water is the primary limiting factor for life and ecosystem processes in polar deserts such as the McMurdo Dry Valleys of Antarctica (Kennedy 1993; Barrett et al. 2007, 2009), this may lead to changes in the system's biotic diversity and activity (Gooseff et al. 2003; Foreman et al. 2004).

Permafrost thaw in the rapidly warming terrestrial arctic has been widely examined for its implications to climate warming feedbacks (Chapin 2005; Bäckstrand et al. 2010), with considerable attention given to soil-atmosphere carbon exchange and the release of carbon by biotic processes in frozen peat soils (Oelbermann et al. 2008; Pautler et al. 2010). Studies on biotic

exchange have generally concentrated on microbial activity and carbon flux, and less on the implications of thawing permafrost for microbial-consuming invertebrates.

However, the ice-free areas of Antarctica (where soils are not covered by snow or ice but other frozen water exists in glaciers and permafrost) are also likely to be altered by regional temperature changes as a result of climatic trends. For example, the region has experienced recent cooling and episodic warming events (Doran et al. 2002; Thompson and Solomon 2002; Barrett et al. 2008b), and warming is projected over longer timescales (Chapman and Walsh 2007; Walsh 2009; Steig et al. 2009). Although permafrost characteristics and extent have been widely studied in the Dry Valleys (Campbell and Claridge 1987; Bockheim et al. 2007; Bockheim 2002), understanding of its relationship with soil biodiversity and soil physical processes remains rudimentary. Furthermore, the effects of temperature changes on a low-diversity system may have a magnified effect on soil biological diversity and ecosystem processes (Ball et al. 2009; Simmons et al. 2009). Because liquid water availability drives biological processes and controls soil development and geochemistry in the Dry Valleys, increased thaw may affect biota directly as well as indirectly through altering soil environmental characteristics that determine habitat suitability for the existing fauna (Lyons et al. 2005; Harris et al. 2007).

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To further investigate the consequences of climate warming on Dry Valley ecosystems, we focused on Taylor Valley, a polar desert in the Ross Sea region, Antarctica (77°S, 162.3°E). Specifically, we examined the interactions between increased moisture likely resulting from permafrost thaw, soil chemical and physical properties, and populations of free-living nematodes, a dominant group of invertebrates in Antarctic soil habitats.

The Dry Valleys are hyper-arid and at the extremes of low biotic temperature and moisture thresholds, restricting species diversity. Soil invertebrates are the system's most prominent fauna, with nematodes typically displaying the highest abundances and dominating the terrestrial food chain (Freckman and Virginia 1997; Powers et al. 1998). The endemic microbial-feeder *Scottinema lindsayae* (Rhabditida) is a particularly common inhabitant of the Dry Valleys, especially in dry, high-salinity soils typical of the landscape (Freckman and Virginia 1997; Courtright et al. 2001). Two other nematode species, the microbial feeder *Plectus murrayi* (Araeolaimida) and the algal feeder *Eudorylaimus antarcticus* (Dorylaimida), are patchily dispersed throughout the valleys and more commonly found in moist areas where algae are present such as lake margins and ephemeral streams (Powers et al. 1998; Barrett et al. 2004; Ayres et al. 2007). Several other metazoan taxa exist in the system including collembolans, mites, tardigrades and rotifers, although at far lower abundances in dry soil habitats and more limited in distribution than nematodes (Powers et al. 1998; Courtright et al. 2001; Stevens and Hogg 2002). Nematode abundance also tends to be greatest in the top 10 cm of soils, decreasing sharply below that point and virtually absent at depths greater than 20 cm (Powers et al. 1994).

Liquid water is unavailable to biota until the austral summer, when permafrost thaws and glacial melt-streams flow across soils, expanding onto soil from perennially ice-covered lakes (Barrett et al. 2009). Thus, the austral summer can be a period of relatively high biological activity (Moorhead et al. 1999). The minimal snow that falls in the valleys (<50 mm water equivalent annually; Fountain et al. 2010) quickly sublimates and rarely moistens soils long enough to become available to soil animals (Gooseff et al. 2003). Nematodes, tardigrades, and rotifers survive in these arid soils by entering into a metabolically inactive state, anhydrobiosis, during periods when liquid water is absent (Treonis et al. 1999; Treonis and Wall 2005; Adhikari et al. 2010). Once liquid water becomes available they resume activity, affecting rates of soil carbon cycling and ecosystem processes (Gooseff et al. 2003; Barrett et al. 2009).

The landscape in the Dry Valleys is underlain by ice-cemented or dry permafrost generally between 20 and 60 cm below the soil surface (Bockheim 2002). Soils are predominantly alkaline, coarse-textured (typically 95–99% sand), and saline (Campbell and Claridge 1987; Poage et al. 2008). Vegetation and primary production is limited to algae and mosses in areas of elevated soil moisture, and intermittent single-celled autotrophs in soils (Johnston and Vestal 1991; Barrett et al. 2005). As a result, organic carbon input into the system is low (Burkins et al. 2000; Hopkins et al. 2006). Given the negligible autotrophic community and organic matter input, rates of biotic activity are slow and heavily influenced by temperature and moisture (Moorhead et al. 1999; Barrett et al. 2006; Zeglin et al. 2009).

We predicted that an increase in available water from thawing permafrost would alter soil physical and chemical characteristics and increase habitat suitability for biota (Courtright et al. 2001; Yeates et al. 2009). Short-term, intensified soil moisture often results in increased biological activity in other desert systems (Noy-Meir 1973; Schwinning and Sala 2004), and has led to changes in soil chemistry across many terrestrial ecosystems including the Dry Valleys (Austin et al. 2004; Barrett et al. 2008b). Additionally, repeated freeze–thaw cycling over time can increase

soil mechanical weathering via cryoturbation processes in polar ecosystems, which also contribute to shifts in chemical characteristics (Bockheim 2002; Ugolini and Bockheim 2008). Therefore, changes in soil properties that determine habitat suitability for soil animals such as soil texture, salinity, pH, and organic matter availability may be found in areas of recurrent permafrost thaw.

Temperatures during the 2008–2009 austral summer were unusually warm for the system, and visible patches of heightened soil moisture on the soil surface indicated the occurrence of subsurface ice melt. Such thawing is likely to fluctuate in magnitude over long timescales (Campbell and Claridge 1987; Lyons et al. 2005), and presumably occurs more frequently in particular micro-sites due to their topographic positions in the landscape and soil characteristics (Campbell and Claridge 1987). We used these distinctly wetted patches across the landscape to compare soil characteristics and biotic make-up in seeps with those of adjacent dry soils. We hypothesized that the abundance and diversity of nematodes would be greater in soils wetted more frequently and for longer durations, coinciding with altered soil conditions potentially more favorable for metabolic processes.

Materials and methods

Site description

Taylor Valley is an ice-free terrestrial ecosystem in East Antarctica and the primary location of the United States National Science Foundation McMurdo Dry Valleys Long Term Ecological Research program (MCM LTER). Mean summer temperatures are around -8°C , and reach above-freezing temperatures for a maximum of three months, beginning in early December and lasting until late February (Doran et al. 2002). Three hydrologic basins separated by glaciers exist across Taylor Valley, which extends from the polar plateau down to the McMurdo Sound. As the three basins each contain distinct soil characteristics, we selected two of the basins for sampling locations near long-term experimental plots of the MCM LTER, Lake Fryxell Basin (77°38'S, 163°06'E) and Lake Hoare Basin (77°37'S, 162°52'E). The Fryxell basin tends to contain higher diversity and abundances of soil organisms, with soils containing higher moisture and organic matter content and lower salinity than Lake Hoare soils (Virginia and Wall 1999; Barrett et al. 2007).

Experimental design and treatments

Samples were collected at the South side of Lake Hoare (hereafter referred to as 'SSLH') and near the F6 Stream at Lake Fryxell ('F6'). We selected three sites in each basin where a permafrost seep was present (soil surface was visibly moistened; termed 'seeps'), and paired these sites with a nearby area of dry soil ('dry soil' sites). Prior to creating soil pits, we took a sample (roughly 5 g) from the surface to measure chlorophyll *a* content, which was used as a proxy for algal biomass and level of primary productivity taking place (Barrett et al. 2004). Soil pits (square-shaped and approximately 40 cm by 40 cm) were dug at each of the paired sites to the depth of the ice-cemented soil. Soil samples were taken at 10 cm depth increments, generally down to 30–40 cm, and soil removed from the pit was placed on a nearby tarpaulin to be replaced in pits after sampling. Pairs of seep and dry pits were distant enough to exhibit a moisture difference, but also close enough so as not to be influenced by other factors such as topography and spatial heterogeneity of soils (generally around 1 m apart).

Soil samples (roughly 500 g) were taken on two opposite sides of the interior of the soil pit using a sterile plastic scoop. The samples were collected in 10 cm increments from the surface down to and including the top of the frozen layer. Soils were placed in

sterile Whirlpack® plastic bags, mixed gently, and transported to the Crary Laboratory at McMurdo Station in insulated ice chests. Prior to sampling, soil temperature was measured with a thermometer at each depth increment and the depth to the layer of ice cement was recorded.

Laboratory analysis

The 5 g surface soil samples were measured for chlorophyll *a* content by the acetone extraction/flourometric procedure (Barrett et al. 2004).

A 100 g sub-sample was removed from each sample under a sterile laminar flow hood within 48 hours of return to the lab and nematodes were extracted by wet-sieving soils and placing in a sugar solution to be centrifuged (Freckman and Virginia 1993). With the aid of an inverted microscope (100–400×), we enumerated and identified nematodes to species, sex and life stage (juvenile/adult and live/dead). Nematodes were reported as total abundance kg⁻¹ dry soil, and as percentages of these totals that were found living.

Gravimetric soil moisture was determined by weighing out a 50 g subsample and drying at 105 °C for 48 h. Remaining soils were placed in freezers in a series of increasingly colder temperatures over a one week period, until they reached –20 °C.

After shipping frozen samples to Colorado State University, an Accumet model 25 pH meter (Fisher Scientific, Pittsburg, PA, USA) was used to measure soil pH by creating a 1:2 saturated paste (30 g soil to 60 mL deionized water) and homogenizing the suspension (Parsons et al. 2004). 90 mL DI water was then added to the suspended soils and an electrical conductivity meter (YSI 30 model, YSI Incorporated, Yellow Springs, OH, USA) was used to measure electrical conductivity (EC) as a proxy for salinity (Parsons et al. 2004).

Soil was sieved through 2 mm mesh and texture measurements were determined by air-drying 50 g soil and adding 50 g/L sodium-hexametaphosphate. The suspension was shaken for 18 hours and temperature was recorded, after which contents were again mixed thoroughly; using a Bouyoucos scale hydrometer we took readings after 40 s to measure silt and sand and after 7 h to measure clay content (Gee and Bauder 1986). Total carbon and nitrogen content was determined using a Leco® TruSpec® (Leco Corp., St. Joseph, MI, USA). Inorganic carbon was also measured, using the modified pressure-calimeter method described by Sherrod et al. (2002).

Statistical analysis

To ensure that measures were representative of individual pits, values from opposing sides of each pit were combined prior to analyses of variance (ANOVA), which was used to assess individual and interacting effects of basin, treatment, and depth increment on soil characteristics and nematode populations. Nematode abundance, EC, and soil moisture were log(*n* + 1) transformed prior to analyses to meet assumptions of normality. Calculations for population structure (specifically, ratios between juveniles, males and females) and community structure could not be performed due to the prevalence of samples with zero values for nematode abundance, and the absence of *E. antarcticus* and *P. murrayii* individuals in nearly all samples. As a result, statistical analyses were not run on these data.

Texture data were arc-sin square root transformed, and measurements of depth to frozen soil were rank-transformed to meet ANOVA assumptions. Modified Bonferroni corrections (Sidack's method) were applied to depth analyses and interactions between location, depth, and treatment effects to compensate for

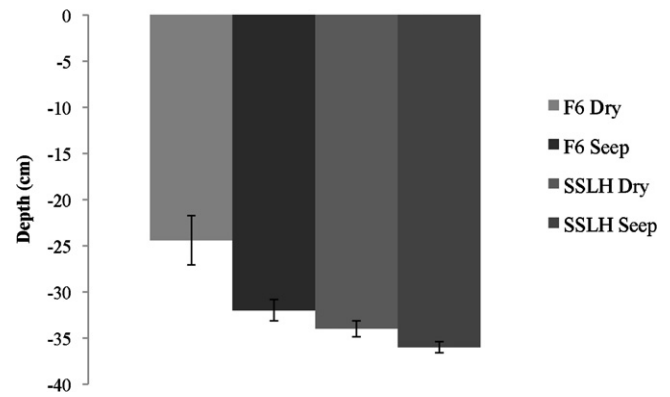


Fig. 1. Depth (mean ± standard error) from the soil surface to the top of the permafrost layer (cm).

multiple-comparison biases. All statistical tests were performed using JMP software (SAS Institute, Cary, North Carolina).

Results

Soil moisture and depth to permafrost

The two basins differed significantly in depth to the ice cemented soil (Fig. 1). Frozen soils occurred at greater depths at SSLH than at F6 (Fig. 1), with average values of 35 cm at SSLH and 28 cm at F6. In addition to differences in depth to frozen soil between the two basins, seep sites were significantly deeper than those measured in dry soils and there was no interaction between these two factors. The mean depths for seep versus dry sites at F6 were 32 cm and 24 cm, respectively. Mean depth in seep soils at SSLH was 36 cm, and 34 cm in dry soils.

Across treatments, F6 soils had significantly higher soil moisture content than those at SSLH (Table 1). Furthermore, there was a much greater difference in moisture content between seep sites and dry sites at F6 than was measured at SSLH (Fig. 2). Whereas mean moisture values for each soil depth increment at SSLH seep sites ranged from 6.6% to 10.1%, seep sites from F6 ranged from 14.9% to 29.5%. Dry treatment soils at SSLH contained depth increment means between 1.4% and 11.5% moisture, and those at F6 contained between 5.5% and 14%.

Soil moisture increased significantly with depth across both basins and treatments ($p < 0.01$), although there was no interaction between depth and treatment. At SSLH, moisture in seep sites increased between the first two increments, from a mean of 6.6% at

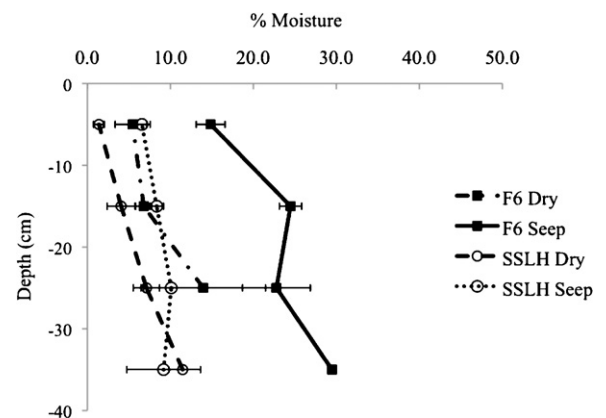


Fig. 2. Percent gravimetric soil moisture content (mean ± standard error) at each depth increment.

Table 1
ANOVA table showing *F*-values for the effects of location, treatment, depth, and interaction effects on total nematode abundance and soil properties (gravimetric soil moisture content, pH, EC, and percentage of sand, silt and clay particles); **p* < 0.05, ***p* < 0.01, ****p* < 0.001 (corrected for multiple comparisons).

ANOVA							
Effect	% moisture	Total nematode abundance	pH	EC	% sand	% silt	% clay
Location	31.000 _{1,33} ***	0.435 _{1,33}	99.273 _{1,33} ***	94.547 _{1,33} ***	28.107 _{1,32} ***	38.143 _{1,33} ***	11.529 _{1,32} **
Treatment	38.626 _{1,33} ***	173.482 _{1,33} ***	54.804 _{1,33} ***	93.581 _{1,33} ***	26.329 _{1,32} ***	56.084 _{1,33} ***	4.503 _{1,32} *
Location × treatment	0.360 _{1,33}	.435 _{1,33}	52.614 _{1,33} ***	41.282 _{1,33} ***	9.172 _{1,32} *	22.238 _{1,33} ***	0.115 _{1,32}
Depth	8.194 _{2,33} **	9.869 _{2,33} ***	4.532 _{2,33}	7.186 _{2,33} **	0.911 _{2,32}	0.453	0.892 _{2,32}
Location × depth	0.141 _{2,33}	0.404 _{2,33}	0.248 _{2,33}	2.275 _{2,33}	0.550 _{2,32}	0.023	1.318 _{2,32}
Treatment × depth	1.591 _{2,33}	4.728 _{2,33}	0.008 _{2,33}	3.593 _{2,33}	0.982 _{2,32}	1.325	2.208 _{2,32}

0–10 cm to 8.4% at 10–20 cm. After 10–20 cm, moisture remained fairly constant down to the 30–40 cm increment; thus, the statistical means for the dry sites in the basin surpassed those of the wet treatments at the 30–40 cm depth (Fig. 2).

Nematodes

Total nematode abundances did not significantly differ between SSLH and F6. However, seeps in both basins had significantly fewer total nematodes present (*p* < 0.001, *F* = 173.482_{1,33}). Nematodes were virtually absent in seeps at F6 and no living individuals were found, whereas dry sites in the basin contained as many as 4308 nematodes per kg dry soil, with a range of around 75–100% live across all depths. At SSLH, dry sites contained a mean percentage of living nematodes of 49% and an average of 53% in seeps (Table 2). *S. lindsayae* was the most prevalent species across all locations, treatments and depths, and was the sole metazoan species in nearly all samples collected. Although very few *E. antarcticus* and *P. murrayii* individuals were encountered across all samples, the soils containing these two genera were collected from dry sites. There did not appear to be any patterns in life stage composition (e.g. ratios of juveniles to adults) across treatments, depths, or locations (Table 2).

With depth, nematodes in both wet and dry sites decreased sharply at both locations beginning at the 10–20 cm increment down to the permafrost layer. The highest nematode abundances found below the surface layer were in the 10–20 cm depths in SSLH dry soils, where moisture levels remained at virtually the same values as those in the surface increment (Fig. 3).

Soil biogeochemical properties

Electrical conductivity varied dramatically between the two basins (*p* < 0.001), with F6 soils having as low as 38 μS and reaching

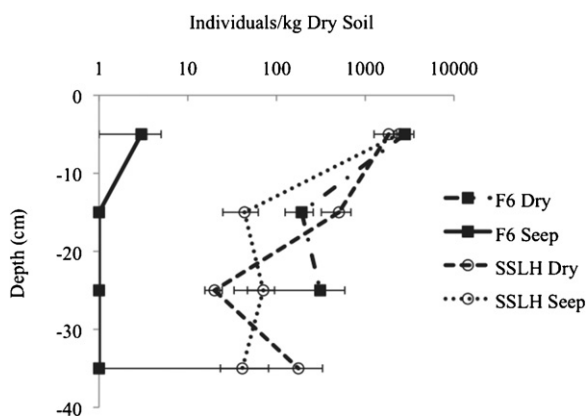


Fig. 3. Total nematode abundances (mean ± standard error) at each depth including the frozen soil layer, in numbers of individuals/kg dry soil. Data are presented on a log scale.

up to 4600 μS. In contrast, soils at SSLH were nearly all between 34 and 100 μS, with the maximum being 150 μS. Lower pH levels were recorded at F6 (*p* < 0.001), ranging from 7.4 to 10.2. Soils from SSLH ranged from pH levels of 9 to 10.2.

Seep sites had significantly higher EC than dry soils (*p* < 0.001) and contained significantly lower pH (*p* < 0.001, Table 1). Across all depths, EC in F6 soils averaged 97 μS, while seep soils averaged 1695 μS. Seeps at SSLH also contained higher EC than dry sites, although the difference was less pronounced than at F6. SSLH dry sites ranged from 35 to 81 μS (mean = 58), while seeps in this location contained a mean EC of 92 μS and ranged from 78 to 121 μS.

EC decreased significantly with depth across all sites; this effect was subtle in SSLH wet and dry soils and F6 dry soils, but sharp between the 0–10 and 10–20 cm increments in F6 wet soils (Fig. 4). Furthermore, there was a slight pattern in interactive effects of treatment and depth, as wet sites at both basins contained higher EC values than dry sites at the 0–10 cm depth increment. This interaction was most notable at F6 and not significant after correcting for multiple comparisons. Although pH decreased slightly in all sites other than F6 seeps (Fig. 5), depth effects had no significant association with the effects of pH.

No trends were observed for chlorophyll a content, or for makeup of inorganic and organic carbon and nitrogen and thus data are not discussed.

Soil texture

The two locations varied significantly in their sand, silt, and clay particle distribution (*p* < 0.001, *p* < 0.001, and *p* < 0.01, respectively). Texture at F6 was more variable than SSLH and in general made up of more clay (*p* < 0.001). Depth increment means for the clay fraction at F6 ranged from 7.5% to 14.8% clay particles as compared to a range of 7–11.9% at SSLH (Table 3).

In addition to differences in soil texture between the two basins, seep presence had a further effect on makeup of sand, silt and clay particles. Seep soils had far lower sand content and higher clay content than dry soils at both SSLH and F6 (*p* < 0.001), the

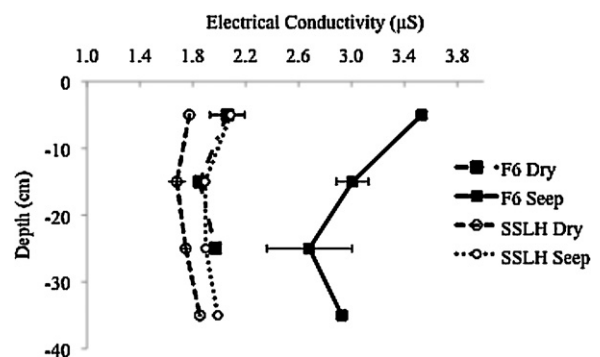


Fig. 4. Electrical conductivity⁻¹ (mean ± standard error) at each depth increment (μS).

Table 2

Soil textures across locations, depths and treatments (percentage of sand, silt, and clay particles). Standard errors are given in parentheses. Dashes indicate no data.

Site	Depth (cm)	F6				SSLH			
		% sand	% silt	% clay	Sample size	% sand	% silt	% clay	Sample size
Dry	0–10	88.83 (4.2)	2.8 (2.0)	8.3 (3.2)	3	92.7 (2.3)	0 (1.1)	7.5 (1.3)	3
Seep	0–10	59.83 (10.9)	25.3 (9.9)	14.8 (1.4)	3	88.8 (1.6)	1.5 (0.5)	9.7 (1.3)	3
Dry	10–20	91.33 (4.8)	1.2 (1.4)	7.5 (3.3)	3	94.3 (2.3)	0 (1.4)	7.0 (0.9)	3
Seep	10–20	47.2 (8.9)	38.0 (8.3)	14.8 (0.7)	3	86.7 (0.4)	2.8 (0.3)	10.5 (0.7)	3
Dry	20–30	87.33 (10.0)	1.3 (3.3)	11.4 (6.8)	2	92.3 (1.5)	0.3 (0.7)	7.3 (1.5)	3
Seep	20–30	48.0 (14.1)	38 (10.5)	14 (3.7)	3	87.7 (0.9)	2.5 (1.4)	9.8 (0.9)	3
Dry	30–40	–	–	–	–	84.2 (6.3)	6.5 (4.8)	9.3 (1.7)	3
Seep	30–40	77.3	16	6.7	1	85.3 (1.0)	2.8 (1.8)	11.9 (0.8)	2

effect was even greater at F6. Depth was not a significant factor in particle-size distribution, although all soils showed the same trend at increasing depth with the exception of F6 seep soils. Sand particle composition in F6 seeps decreased by about 10% between 0–10 cm and 10–20 cm, but increased again to around 77% at the lowest depths (30–40 cm); seep soils at SSLH also decreased slightly at the 10–20 cm depth, but only by a few percent. In SSLH soils and F6 dry soils, sand content was relatively constant (around 90%). Clay content accordingly showed inverse trends at both basins (Table 3).

Discussion

Our seep sites were associated with distinct soil properties and populations of soil nematodes relative to reference soils more typical of Taylor Valley (e.g. Barrett et al. 2004). Higher moisture levels were correlated with lower pH, higher conductivity and higher clay content, indicating that the moisture increases seen in seeps alter interactions between multiple soil characteristics, the degree of variation in each of the above soil properties commensurate with level of moisture increase.

Typically, soils at F6 are a more suitable habitat for nematodes and contain more abundant and diverse communities (Barrett et al. 2004). The soil properties found for dry soils in the current study are consistent with other research in the Dry Valleys in terms of soil chemical and physical characteristics as well as soil nematode abundances (Freckman and Virginia 1997; Powers et al. 1998; Courtright et al. 2001; Poage et al. 2008). However, we show here that soils in seepage sites, particularly at F6, deviate significantly from dry soils in terms of soil properties (Table 1).

Our results are also consistent with previous research carried out in the region focusing on moisture, salinity and pH as major determinants of nematode distribution and viability (Powers et al. 1998; Courtright et al. 2001; Nkem et al. 2006), and dependence of nematodes on these specific environmental conditions for functioning (Gooseff et al. 2003; Barrett et al. 2008a). A recent study

investigated temperature and moisture additions to surface soils over an eight-year period in the Dry Valleys, as well as a naturally occurring glacial melt event that flooded experimental plots during one season of the long-term study (Barrett et al. 2008b; Simmons et al. 2009). The authors observed that *S. lindsayae* responded poorly to the micro-climate manipulations and natural flood event, while *E. antarcticus* responded favorably (although not immediately). They concluded that such habitat shifts over longer timescales might impact individual species differently, altering food-web dynamics and thus nutrient cycling. Results of the present study expand on these previous conclusions by identifying a separate aspect of potential impacts on polar desert ecosystems under projected climate change; specifically, seasonally heightened moisture content resulting from increased below-ground thaw.

Beyer et al. (1999) attributed soil development in the Antarctic Dry Valleys primarily to cryoturbation, acidification, and mineral weathering among several other chemical processes. Our study exemplifies this in that we saw differences in clay particle content and pH, both of which are by-products of soil development processes and contribute to nematode habitat suitability. A study by Barrett et al. (2004) showed that polygon formation in soils across the landscape, a direct result of cryoturbation and areas in which soil movement and weathering are high, differed in both soil properties and nematode abundances. Specifically, they observed nematodes at greater abundances in the interior of polygon features, with fewer in the troughs between polygons where churning and development of soils actively occurs.

While freeze–thaw processes occur to a certain extent each summer, they are thought to vary in degree over longer timescales in response to annual and seasonal variability in temperature and moisture (Campbell and Claridge 1987). This observation suggests that varied magnitudes of freeze–thaw events over time have led to shifts in soil characteristics, such as those observed in the current study. Seeps tend to occur in relatively consistent locations throughout the valley through time, as topographic positions on hillsides determine exposure to both sun and aeolian soil deposition, determinants of depth to which soils remain frozen (Campbell and Claridge 1987).

Our study suggests that increased permafrost thaw may contribute to soil change throughout the active layer, most notably through weathering. While temperatures reached during summer months are in most years too subtle to significantly alter thaw extent (Campbell and Claridge 1987), they would become more effective in promoting weathering over time under gradual warming scenarios and increases in the intensity, frequency, and spatial extent of moisture pulses (Harris et al. 2007). The observation of increased patches of moisture during relatively high-temperature years (Lyons et al. 2005; Harris et al. 2007) suggests that higher than average ice melt is occurring belowground and supports this projection.

The increased salinity in the seeps is likely a result of evapo-concentration. As permafrost thaws, salts are mobilized and carried up through the soil profile. While the moisture that is drawn up to

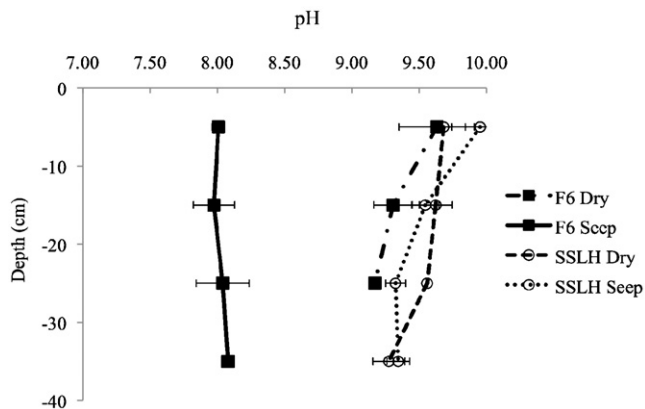
**Fig. 5.** Soil pH (mean ± standard error) at each depth increment.

Table 3
Population structure of *S. lindsayae* (percentages of juveniles, males, and females making up total abundance and percentage of total abundance found living), across locations, treatments, and depth increments. “N/A” is listed for samples containing no nematodes; dashes indicate that no sample was taken.

Site	Depth (cm)	F6				SSLH			
		% juvenile	% male	% female	% live	% juvenile	% male	% female	% live
Dry	0–10	68.1	17.3	44.6	84.3	66.9	16.6	51.5	54.7
Seep	0–10	100.0	0.0	0.0	0	80.7	9.5	50.1	65.5
Dry	10–20	68.3	15.2	50.7	64.3	74.3	13.2		53
Seep	10–20	N/A	N/A	N/A	N/A	72.2	10.2	10.2	68.9
Dry	20–30	74.5	15.5	32.4	94.5	58.3	37.5	37.5	54.7
Seep	20–30	N/A	N/A	N/A	N/A	87.9	3.0	3.0	32.8
Dry	30–40	–	–	–	–	65.8	19.9	19.9	35
Seep	30–40	N/A	N/A	N/A	N/A	33.5	3.1	3.1	46.7

the surface through capillary action evaporates, salt ions remain in surface soils and accumulate over time (Lyons et al. 2005). This may also be related to the higher clay content in seeps, as soils with higher clay content support more capillarity action.

While most of our samples showed a consistent relationship between nematode abundance and certain soil properties such as sand and clay content, EC, and pH, two measurements deviated from these patterns. The samples taken from SSLH seeps at the 0–10 cm and 20–30 cm depths had higher mean nematode abundance and mean living to dead ratios than dry soils at those depths. However, the differences in moisture content and soil properties seen between dry and seep samples at SSLH were slighter than those at F6. Despite these exceptions, seeps overall displayed significantly lower nematode abundance and living to dead ratios across basins and depths in comparison with dry soils.

The gradient in soil characteristics and nematode population abundances we observed highlights the concern that, with future rises in temperature, the system may reach a “tipping point” due to changes in ecosystem conditions and thus the functioning of biota (Wall 2007). We found that permafrost thaw is associated with notable differences in soil characteristics such as soil texture, salinity, and pH, suggesting that formerly suitable habitat for soil animals adapted to dry soils may eventually be pushed beyond suitability. Thus, in the future, as permafrost thaw increases in magnitude, frequency and spatial extent, processes that alter soil habitat such as freeze–thaw cycles and evapo-concentration will become more prevalent and the distribution of biota across the landscape may be substantially reduced.

We conclude that increasing levels of permafrost thaw from climate warming will have negative consequences for the Dry Valley biota, which naturally contain minimal diversity due to extreme environmental conditions and have rarely received new species as a result of geographic isolation (Adams et al. 2006). The endemic nematode *S. lindsayae* contributes substantially to carbon cycling. During a recent cooling event (1993–2005), the population size of the species was shown to decrease by greater than 60% directly leading to a decline in soil carbon cycling of as much as 7% (Doran et al. 2002; Barrett et al. 2008a). These findings are concerning and suggest altered biodiversity and distribution of soil fauna with potentially hindered ecosystem functioning under altered environmental conditions.

As in arctic ecosystems (Oelbermann et al. 2008; Pautler et al. 2010) amplified climatic change leading to permafrost thaw may also alter biotic processes in polar deserts of Antarctica. The responses to change by invertebrate communities, which are only now beginning to be investigated, are critical components in understanding these processes. Additional insight on the interactions between soil species, temperature changes, and resulting influences on nutrient dynamics of both frozen and un-frozen soil must be extended further to better predict how various polar systems as a whole might respond to shifts in climate.

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