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Abstract

Soils of the McMurdo Dry Valleys are among the most extreme terrestrial environments, hosting low-diversity food webs of microbes, protozoa, and metazoan invertebrates. Distribution of soil invertebrates, particularly nematodes, is related to the highly variable soil geochemistry of the valleys. Bull Pass is a glacially carved area within the McMurdo Dry Valleys where a broad range of geochemical conditions occurs along a continuous soil gradient. This site provides the opportunity to investigate how soil geochemistry controls nematode distribution on a local scale, and to establish correlations that may also be relevant at regional scales. At Bull Pass, two nematode species were present, with the dominant *Scottnema lindsayae* occurring in >30% of the samples. There were significant negative correlations between live nematode abundance and soil nitrate concentration and salinity, consistent with experiments showing strong salinity effects on nematode survival. A logistic regression model based on data sets from across the McMurdo Dry Valleys showed a strong negative relationship between soil salinity and the probability of live nematodes occurring. Soil chemistry and nematode distribution from the Bull Pass transect are compared with model results and suggest that the larger-scale distribution of nematodes across the McMurdo Dry Valleys may be reflected in the smaller-scale chemical and biological gradients at Bull Pass.

Introduction

High degrees of spatial heterogeneity in soil chemistry and soil biota are common features among dry and extreme ecosystems because the occurrence of organisms, plants, microbes, and invertebrates are strictly limited by resource availability which can vary markedly over a wide range of spatial scales (Charley and West, 1975; Freckman and Virginia, 1989; Virginia et al., 1992; Smith et al., 1994; Schlesinger et al., 1996; Kelly and Burke, 1997; Aguiar and Sala, 1999; Burke et al., 1999; Wall and Virginia, 1999; Kaufmann, 2001; Xie and Steinberger, 2001). The McMurdo Dry Valleys of Antarctica exhibit large spatial variability in soil geochemistry (e.g. Bockheim, 1997) resulting in complex distributions of invertebrate communities (e.g. Virginia and Wall, 1999). One goal of the McMurdo Dry Valleys Long-Term Ecological Research program (MCM-LTER) is to understand the geochemical and climatic factors controlling spatial variability of these invertebrate populations (Virginia and Wall, 1999; Courtright et al., 2001; Barrett et al., 2004) and to establish baseline data from which to monitor long-term fluctuations in their abundance and diversity.

Soil biodiversity is low in the McMurdo Dry Valleys, with nematodes among the most widely distributed invertebrate taxa (Schwartz et al., 1992; Freckman and Virginia, 1997). A number of studies have addressed the geochemical influence on dry valley nematode populations over a range of spatial scales (sub-meter to tens of kilometers), as well as across local landscape gradients (Freckman and Virginia, 1998; Powers et al., 1998; Courtright et al., 2001; Treonis et al., 1999; Gooseff et al., 2003; Barrett et al., 2004). Results are consistent with predictions from a qualitative conceptual model relating habitat suitability and community structure (e.g. nematode presence or absence, population size) to variations in soil salinity, moisture, and organic matter content (Freckman and Virginia, 1998). However, multiple regression and multivariate ordination techniques describing nematode habitat suitability and distribution over environmental gradients have yielded statistical models with limited explanatory power (Freckman and Virginia, 1997; Courtright et al., 2001; Moorhead et al., 2003). These models may be limited because diversity and abundance of nematodes are controlled by many independent edaphic and/or geochemical parameters that vary discontinuously over multiple scales (Barrett et al., 2004).

Here we present a soil geochemistry and nematode population study from the Bull Pass region of the McMurdo Dry Valleys (Fig. 1a). A soil sample transect (Fig. 1b) across the southwestern half of Bull Pass encompasses a continuous soil geochemistry gradient spanning a range of geochemical conditions similar in magnitude to those found across the entire dry valleys region (e.g. Bockheim, 1997). This unique environment allows for a quantitative assessment of the controls that soil geochemistry exerts on the presence or absence of nematode communities, and on various other parameters such as population numbers and mortality.

We developed a logistic regression model based on published data sets from across the McMurdo Dry Valleys describing the probability of live nematode populations occurring given a particular set of soil chemical properties. Objectives in developing this model were to assess how species assemblages are influenced by their physical and chemical environments in the formation of soil communities, and to evaluate the degree to which the spatially confined geochemical gradient at Bull Pass might serve as a scale model for much of the variation in nematode distribution
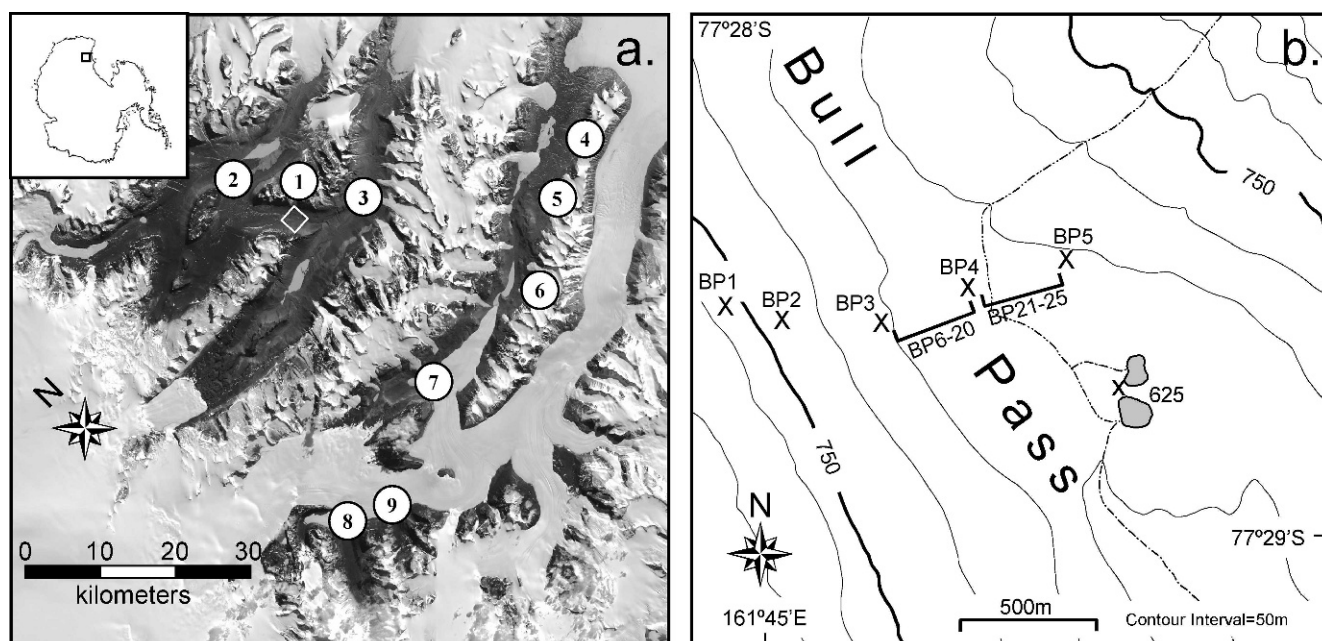
FIGURE 1. (a) Map of the McMurdo Dry Valleys showing sample locations used in the logistic regression model: 1—Bull Pass, 2—Victoria Valley, 3—Wright Valley, 4—Taylor Valley–Lake Fryxell Basin, 5—Taylor Valley–Lake Hoare Basin, 6—Taylor Valley–Lake Bonney Basin, 7—Pearse Valley, 8—Beacon Valley, 9—Arena Valley. The study area is outlined by the white box. (b) Detail of the study area showing sample locations.

observed across all of the McMurdo Dry Valleys. We compare the continuous dataset from Bull Pass with model results and identify threshold conditions for establishment of nematode communities in the extreme dry valleys environment.

The results of this study further our quantitative understanding of the geochemical control over nematode distribution along a well-constrained geochemical gradient and provide a field comparison for recent experiments assessing salinity thresholds for nematode survival (Nkem et al., 2006). In addition, we establish a statistical basis for understanding invertebrate distribution over the entire dry valleys region and suggest that salinity plays a primary role in determining the nematode habitat suitability of a particular soil.

Site Description

The McMurdo Dry Valleys (Fig. 1a) occupy the largest ice-free region of Antarctica and are characterized by climatic conditions among the most extreme on Earth. Mean annual temperatures on the valley bottoms range from −15 to −30°C, and annual precipitation is typically less than 10 cm water equivalent (Fountain et al., 1999; Doran et al., 2002). Valley floors typically have fewer than 50 days where temperatures exceed 0°C (Doran et al., 2002). Consequently, liquid water is unavailable across much of the landscape for most of the year and is a primary limitation to biological activity and soil weathering (e.g. McKnight et al., 1999; Treonis et al., 2002; Maurice et al., 2002).

Arid soils are the most extensive landform of the McMurdo Dry Valleys, occupying 95% of glacier ice-free surfaces below 1000 m (Burkins et al., 2001). Dry valley soils are predominantly glacial tills formed over the past ~8 million years derived from a variety of lithologies including sandstones, mafic intrusive and extrusive rocks, granites, and metamorphic rocks (Denton et al., 1989; Brook et al., 1993; Sugden et al., 1995; Marchant et al., 1996; Marchant and Denton, 1996; Hall and Denton, 2000; Higgins et al., 2000; Campbell, 2003). Soils are typically coarse textured, extremely

low in organic matter content, neutral to alkaline in pH, and often have high salinity broadly correlative to soil surface age (Campbell and Claridge, 1987; Bockheim, 1997; Campbell et al., 1998; Bockheim, 2002; MCM-LTER, unpublished data).

No vascular plants or vertebrates inhabit the McMurdo Dry Valleys; food webs consist of cyanobacteria, algae, bacteria, fungi, yeasts, protozoans, and a few taxa of metazoan invertebrates (Friedmann et al., 1993; Alger et al., 1997; Laybourn-Parry et al., 1997; Freckman and Virginia, 1997; Priscu et al., 1999; Cowan et al., 2002; Bamforth et al., 2005). In most dry valleys soil habitats where invertebrate communities are established, populations are comprised of up to three nematode species with similarly low diversity of rotifers and tardigrades (Freckman and Virginia, 1998; Adams et al., 2006). Nematode species identified in the McMurdo Dry Valleys include the microbial feeders *Scottnema lindsayae* and *Plectus antarcticus*, and the omnivore *Eudorylaimus antarcticus* (Freckman and Virginia, 1991). These species are not distributed uniformly across dry valleys soils. For example, nematode diversity and abundance is highest in the Fryxell basin of Taylor Valley where soil organic carbon concentrations are relatively high, as compared to Beacon and Arena Valleys where soil salinity is high and no nematodes have been found (Freckman and Virginia, 1998).

Bull Pass is glacially carved valley trending approximately NW–SE across the Olympus Range between Victoria and Wright Valleys (Fig. 1a). The broad valley floor is covered predominantly by coarse-textured soils with prominent polygon features (Barrett et al., 2004), which give way to colluvial scree higher up the valley walls. Along the valley floor, exposures of Ferrar Dolerite and granite create a highly variable small-scale topography with a stone pavement surface and sandy soils. Two small ponds occupy depressions on the valley floor. A single active stream from the northeast feeds these ponds; there were no active streams on the southwest flank of the valley near the study area. The geomorphologic history of Bull Pass is not well established, but it may share elements of the complex history of the adjacent

TABLE 1
Sample location and surface soil chemistry.

Sample	Lat. (S)	Long. (E)	Chloride 0–10 cm (ppm)	Nitrate 0–10 cm (ppm)	Sulfate 0–10 cm (ppm)	EC (μS cm^{-1})	pH	Soil Moisture (%)	Organic Carbon (g kg^{-1})	Total Nitrogen (g kg^{-1})
BP 1	77°28.77′	161°44.43′	12.7	0.7	11.2	19	9.15	0.38	0.23	0.02
BP 2	77°28.71′	161°45.22′	17.8	1.3	9.5	19	9.10	0.43	0.27	0.03
BP 3	77°28.62′	161°46.17′	39.1	4.3	30.4	49	9.50	0.16	0.21	0.02
BP 6	77°28.61′	161°46.22′	*28.8*[1]	*3.9*	*24.4*	37	9.63	0.50	*0.20*	*0.03*
BP 7	77°28.60′	161°46.22′	18.6	3.6	18.3	102	8.83	0.32	0.19	0.03
BP 8	77°28.59′	161°46.32′	*29.4*	*5.6*	*29.7*	87	9.09	0.32	*0.22*	*0.03*
BP 9	77°28.58′	161°46.37′	40.3	7.6	41.1	43	9.06	0.30	0.25	0.02
BP 11	77°28.56′	161°46.46′	73.1	18.4	74.4	205	8.62	0.55	0.24	0.02
BP 12	77°28.55′	161°46.51′	n.d.[2]	n.d.	n.d.	787	8.43	0.45	n.d.	n.d.
BP 13	77°28.54′	161°46.55′	2226	666	519	1050	8.22	2.63	0.33	0.47
BP 14	77°28.54′	161°46.61′	n.d.	n.d.	n.d.	7000	7.87	2.86	n.d.	n.d.
BP 15	77°28.53′	161°46.67′	3400	1585	3683	4476	8.02	1.73	0.30	0.15
BP 16	77°28.53′	161°46.71′	n.d.	n.d.	n.d.	4361	7.90	2.65	n.d.	n.d.
BP 17	77°28.53′	161°46.77′	8526	3800	6410	3374	8.13	1.22	0.12	0.35
BP 18	77°28.52′	161°46.82′	n.d.	n.d.	n.d.	2089	8.32	1.39	n.d.	n.d.
BP 19	77°28.52′	161°46.89′	2256	909	7806	2151	8.26	2.59	0.30	0.13
BP 20	77°28.52′	161°46.93′	n.d.	n.d.	n.d.	1663	8.33	1.17	n.d.	n.d.
BP 4	77°28.52′	161°46.97′	1260	461	4431	1406	8.47	1.69	0.22	0.05
BP 21	77°28.52′	161°47.11′	n.d.	n.d.	n.d.	2315	8.13	2.53	n.d.	n.d.
BP 22	77°28.52′	161°47.24′	1552	524	3237	1913	8.30	1.75	0.23	0.06
BP 23	77°28.50′	161°47.51′	n.d.	n.d.	n.d.	3630	8.06	1.61	n.d.	n.d.
BP 24	77°28.48′	161°47.79′	739	246	1777	1061	8.31	0.30	0.21	0.03
BP 25	77°28.45′	161°47.82′	229	65	807	719	8.53	0.25	0.19	0.02
BP 5	77°28.44′	161°47.86′	788	247	129	689	8.63	0.33	0.22	0.02

[1] Italics denotes data interpolated from adjacent samples based on transect distance.

[2] n.d. = not determined.

central Wright Valley. Prentice et al. (1993) summarized the Late Neogene history of central Wright Valley presenting evidence for fjord inundations at ca. 9 Ma and ca. 5.5 Ma, as well as a glacial episode >3.9 Ma that deposited the Peleus till, which occupies portions of the Wright Valley floor below Bull Pass. In addition, Hall et al. (2001) presented evidence for the Late Pleistocene to Holocene aged Glacial Lake Wright. However, it is unclear how these events directly affected surface exposure ages, geomorphology, or soil chemistry in our study area because the highest elevation evidence reported in these studies is 566 meters a.s.l., well below the lowest elevation point on our sample transect.

Sampling and Laboratory Methods

Soil samples were collected along a ~1500 m transect (~130 m relief) spanning the southwest half of Bull Pass (Fig. 1b) in two phases during the 2004–2005 field season. Soil pits were dug down to ice-cemented ground (~25–35 cm) with ~500 g sampled at incremental depths using a single acid-washed plastic trowel per soil pit. Samples were sealed in Whirl-Pak bags and transported from the field to Crary Laboratory at McMurdo in ice chests and stored at 4°C until processed.

Soil salinity was estimated by measuring the conductivity of a 1:5 solution of the <2 mm size fraction in DI water using a calibrated Yellow Springs Instrument 3100 conductivity meter. We measured soil pH on 1:2 saturated paste of the <2 mm size fraction in DI water using an Orion model 720A pH meter. Gravimetric soil moisture was determined on samples dried in a forced air oven at 105°C for at least 48 hours. Inorganic nitrogen samples were extracted in 50 mL of 2 M KCl, shaken for 30 minutes on an orbital shaker at 250 RPM, and filtered through

Whatman No. 42 filter paper. These samples were analyzed on a Lachat colorimetric autoanalyzer. Anion analytes were prepared on 1:5 DI extracts, shaken for 30 minutes on an orbital shaker, and filtered through Whatman No. 42 filter paper. These samples were analyzed for Cl^- and SO_4^{2-} using a Dionex ion chromatograph. Soil organic carbon and total soil nitrogen were determined on acidified (6 N HCl) ball mill-ground splits of the <2 mm size fraction using a Carlo Erba 1500 elemental analyzer. All analytical measurements were performed in the Dartmouth College Environmental Measurements Laboratory. For purposes of correlation with invertebrate population data, soil geochemical results are reported as the weighted average of the <10 cm samples.

For invertebrate samples, approximately 500 g of soil were collected from 0–10 cm depth using individual aseptic plastic trowels to avoid cross-contamination. The 0–10 cm sampling was chosen, as earlier studies have shown that invertebrates preferentially inhabit the upper 10 cm of most dry valleys soils (Powers et al., 1995). Quantitative characterization of invertebrate communities was conducted at McMurdo Station, usually within 48 hours of sample collection. Approximately 100 g of soil were processed for living and dead nematodes, rotifers, and tardigrades using the sugar centrifugation technique modified from Freckman and Virginia (1993). Nematode species were identified on the basis of morphology using inverted light microscopy, and categorized by sex, life stage (adult, juvenile), and as living or dead based on observations of movement and morphology.

As the McMurdo Dry Valleys include many soils that harbor no invertebrate species (e.g. Freckman and Virginia, 1998; Bamforth et al., 2005), we developed a logistic regression model from >700 soil samples from previous dry valleys studies to account for the presence or absence of nematode species based
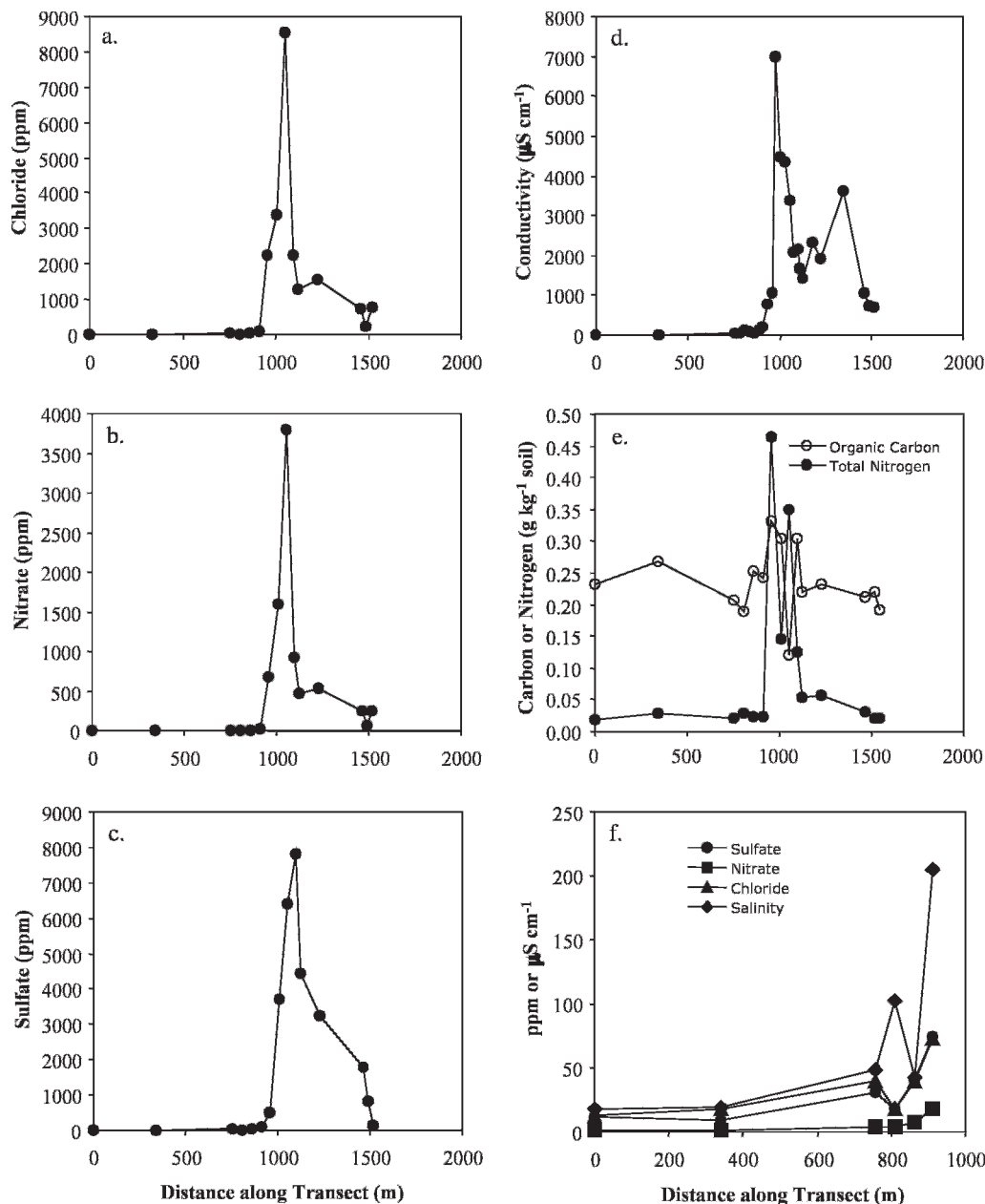
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FIGURE 2. Soil geochemistry along the ~1500-m sampling transect in Bull Pass. Figure 2f is an expanded view from 0 to 900 m where most variation in nematode populations occurs.

upon a suite of soil properties, specifically soil moisture content, electrical conductivity as a proxy for salinity, soil organic carbon, and total soil nitrogen. Such a large data set of other geochemical parameters such as soil nitrate, chloride, and sulfate is not currently available and is not included in the model. Six valley systems are represented in this data set (Fig. 1a), with the majority (~84%) of observations from Taylor Valley where the MCM-LTER maintains core experiments. Multiple sites are included from the Lake Fryxell ($n = 170$), Lake Hoare ($n = 279$), and Lake Bonney basins ($n = 142$) within Taylor Valley (Powers et al., 1998; Treonis et al., 1999; Courtright et al., 2001; Gooseff et al., 2003; Moorhead et al., 2003; Barrett et al., 2004; Parsons et al., 2004; Nkem et al., 2006; MCM-LTER, unpublished data [http://huey.colorado.edu/LTER]). Additional sites were included from Wright Valley ($n = 27$; Courtright et al., 2001), Victoria Valley ($n = 27$; Courtright et al., 2001), Pearse Valley

($n = 15$; MCM-LTER, unpublished data), Beacon Valley ($n = 8$; Nkem et al., 2006) and Arena Valley ($n = 17$; Nkem et al., 2006).

Logistic regression models follow the general form:

$$\log(P/[1-P]) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 \ldots, \quad (1)$$

where P is the probability of encountering a particular species, α is the intercept, and β is the slope parameter of the explanatory variable x. We used the logistic regression procedure in SAS v9.1 with stepwise selection of explanatory variables for the two nematode species found at Bull Pass, *S. lindsayae* and *E. antarcticus*, individually determined by a statistical significance threshold of $p < 0.05$. The logistic procedure fits linear logistic regression for binary responses (presence or absence) by the process of maximum likelihood estimation with the Fisher-scoring algorithm.

Sample	*Scottnema lindsayae*				*Eudorylaimus antarcticus*			
	Live Total (#/kg dry soil)	Sex Ratio (M:F)	Mortality	Fecundity	Live Total (#/kg dry soil)	Sex Ratio (M:F)	Mortality	Fecundity
BP 1	1567	0.83	0.21	1.57	0	NA	NA	NA
BP 2	4688	0.78	0.15	2.22	0	NA	NA	NA
BP 3	5165	0.72	0.07	1.11	0	NA	NA	NA
BP 6	680	1.58	0.45	3.00	51	1	0.80	3.00
BP 7	90	1.00	1.33	2.50	0	NA	NA	NA
BP 8	170	4.00	1.06	3.50	10	NA	0.00	NA
BP 9	324	1.22	0.39	1.44	10	NA	1.00	NA
BP 11	20	NA	2.00	NA	0	NA	NA	NA

Results and Discussion

SOIL GEOCHEMISTRY

The soil geochemistry in Bull Pass exhibits large variation across the sample transect (Table 1; Fig. 2). Chloride values ranged from 12.7 to 8526 ppm; nitrate and sulfate values ranged from 0.7 to 3800 ppm and 9.5 to 7806 ppm, respectively. Gravimetric soil moisture values ranged from 0.16% to 2.86%. Soil organic carbon and total soil nitrogen exhibit similar variability with concentrations from 0.12 to 0.33 g kg^{-1} and 0.02 to 0.47 g kg^{-1}, respectively. Soil conductivity ranged from 19 to 7000 µS cm^{-1} and soil pH ranged from 7.9 to 9.63. There was a strong negative logarithmic relationship between soil conductivity and pH reflecting the electrode-specific influence of dissolved salts on the measured pH values. The magnitude of these geochemical variations approaches those found across previously analyzed soils over most of the McMurdo Dry Valleys (Bockheim, 1997; Powers et al., 1998; Freckman and Virginia, 1998; Courtright et al., 2001; Barrett et al., 2004; Nkem et al., 2006; MCM-LTER, unpublished data).

Figure 2 summarizes the spatial variability in soil physicochemical parameters across the sampling transect. Anion concentrations (Figs. 2a–2c) and conductivity (Fig. 2d) showed moderate increases between 0 and ~900 m along the transect. Values increase sharply to a peak between 1000 and 1100 m. These peak values are followed by subsequent large declines toward the end of the transect at ~1550 m where anion concentrations and conductivity are significantly lower than peak values but are still elevated above background levels established by higher elevation samples. Organic carbon and total soil nitrogen concentrations broadly follow similar trends (Fig. 2e) but do not show as pronounced proportional increases across the first 900 m of the transect. Soil moisture is lower (<0.55%) in the higher elevation samples, increasing to 1–3% between 900 and 1400 m before dropping sharply at the end of the transect. The cause of this soil moisture trend is unknown; one possibility is that higher salt concentrations in these soils may improve water retention. Figure 2f shows an expanded view of salinity and anion concentration data for the first 900 m of the transect where most variability in nematode population data occurs.

The gradual increase in anion concentrations over the first 900 m (Fig. 2f) is consistent with leaching and systematic downslope redistribution of soluble anions, changing atmospheric inputs with elevation change, and/or wind-driven uphill redistribution of more saline surface soil material. The sharp increase in anion concentrations past 900 m could also result from soil leaching and downslope accumulation; however, in the absence of meltwater streams, these processes are probably negligible

(Claridge et al., 1997). Alternatively, salt precipitation along the evaporative margin of an ancient pond, similar to those on the valley floor near the sampling transect (Fig. 1b), may have produced high salinity soils. Such soils are commonly found adjacent to streams and lakes elsewhere in the McMurdo Dry Valleys (Barrett et al., 2002). There are no obvious geomorphologic features at this site associated with ancient lake margins, such as strandlines or deltas (e.g. Hall et al., 2001). It is possible that they are obscured by the irregular topography created by igneous rock outcroppings near the valley floor. $Cl^-{:}SO_4^{2-}$ and $NO_3^-{:}SO_4^{2-}$ ratios shift rapidly from higher to lower values at ~1100 m and are consistent with early precipitation of gypsum at an evaporative pond margin, but these shifts may also be caused by preferential leaching and redistribution of chloride and nitrate. Irrespective of its origin and history of modification, the well-defined Bull Pass geochemical gradient provides the opportunity to assess the relationships between continuously changing soil geochemistry and extant invertebrate populations.

NEMATODE POPULATIONS

Invertebrate communities included the endemic nematodes *S. lindsayae* and *E. antarcticus*. Other metazoan invertebrates reported for soils in the McMurdo Dry Valleys (rotifers, tardigrades) were not recovered from any samples. Nematodes were only found in samples collected from 0–900 m along the transect. Abundance, sex ratio, mortality, and fecundity data from these samples are summarized in Table 2. *S. lindsayae* was present in all eight samples where nematodes were found and accounted for >90% of individuals found in two-species communities. Abundance of *S. lindsayae* varied from 0 to >5000 live individuals per kg soil with live population density decreasing with distance along the transect, eventually reaching zero past ~900 m (Fig. 3). *E. antarcticus* was found in only 3 of the 25 samples for which nematodes were extracted, where it was present in low numbers (10–51 kg^{-1} soil). The sex ratio (M:F) of *S. lindsayae* averaged 0.78, with proportionally more females occurring at higher elevations shifting sex ratios to >1 past ~750 m. Nematode mortality (dead:live individuals) ranged from 0.07 to 2.00 with values generally increasing farther along the transect (Fig. 3). Fecundity (live juveniles/live females) ranged from 1.11 to 3.50 (mean = 2.2) and showed no consistent trends along the transect.

Spatial heterogeneity in dry valleys soil geochemistry encountered over broad scales complicates interpretation of invertebrate population response to variation in soil chemistry. In the case of Bull Pass, the relatively short transect distance eliminates many potentially confounding variables, allowing for a more direct evaluation of the effects of soil chemistry. Strong

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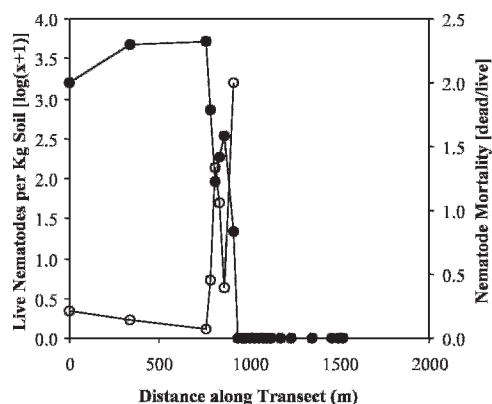
FIGURE 3. Live individuals of *S. lindsayae* per kilogram of soil (solid circles; plotted as log[x + 1]) and *S. lindsayae* mortality (open circles) plotted against distance along the sampling transect. A sharp decrease in abundance between from ~750 to 900 m is accompanied by a sharp increase in mortality.

covariation between changes in soil chemistry and changes in *S. lindsayae* abundance and population parameters suggest direct geochemical control over the viability of *S. lindsayae* communities. *E. antarcticus* occurs with sufficient infrequency that comparisons with soil geochemistry are not practical.

Table 3 is a Pearson correlation matrix for selected geochemical and biological parameters for the Bull Pass samples that contained *S. lindsayae*. There are significant correlations between nitrate concentration and both live *S. lindsayae* abundance ($R = -0.75$; $P < 0.05$) and *S. lindsayae* mortality ($R = 0.77$; $P < 0.05$). Soil conductivity, which is a function of anion concentration, correlates even more strongly with live *S. lindsayae* abundance ($R = -0.86$; $P < 0.01$) and mortality ($R = 0.95$; $P < 0.01$), reflecting the combined influence of sulfate, chloride, and nitrate on soil salinity (Fig. 4). Soil pH also correlates strongly with *S. lindsayae* abundance ($R = 0.73$; $P < 0.01$) and mortality ($R = -0.76$; $P < 0.01$) but likely results from systematic variation in pH measurements associated with conductivity. These correlations suggest that progressive increases in anion concentrations (particularly nitrate), collectively reflected in the conductivity values, create progressively more inhospitable soils for *S. lindsayae* communities along the Bull Pass transect. Soil moisture, organic carbon, and total soil nitrogen were less well correlated with nematode population parameters, and presumably, within the range of observed values exert less influence on the viability of nematode communities.

Our data corroborate recent laboratory experiments evaluating the salt tolerance of two endemic nematode species, *S. lindsayae* and *Plectus antarcticus* (not found at Bull Pass) (Nkem et al., 2006). This study documented the effects of salinity and salt composition on nematode survival in laboratory-prepared salt solutions and saturation paste extracts from dry valleys soils. The results are not quantitatively comparable to our field results, as lab experiments cannot replicate the complicated and fluctuating hydrology of dry valleys soils; however, there are similarities. In the laboratory experiments, variations in salt solution strength (and conductivity) generate very steep response curves with respect to nematode survival. This suggests a salinity threshold above which the soil environment is sufficiently inhospitable as to limit survival (Nkem et al., 2006; their Fig. 2). The geochemical gradient at Bull Pass generates a similar response with viable *S. lindsayae* populations occurring in soils with conductivities up to ~50 μS cm^{-1}, declining rapidly such that no living nematodes are found in soils with conductivities above ~200 μS cm^{-1}. In addition, Nkem et al. (2006) showed a salt-specific effect with nematode survival most strongly influenced by nitrate salts, and to a lesser degree by chloride or sulfate salts. Consistent with this observation are the stronger correlations in the Bull Pass dataset between soil nitrate and both live nematode abundance and mortality as compared to sulfate or chloride.

LOGISTIC REGRESSION MODEL FOR DRY VALLEYS NEMATODES

Presence of the most frequently encountered nematode species, *S. lindsayae*, was significantly related to soil conductivity, soil moisture content, and total soil nitrogen (Table 4), accounting for 60% of the total variation in *S. lindsayae* distribution. A logistic model describing the distribution of *E. antarcticus* as a function of soil conductivity, moisture, and organic carbon content was also significant, though less robust, accounting for 32% of variation in *E. antarcticus* distribution (Table 4).

Figure 5 illustrates the change in the probability of encountering either *S. lindsayae* or *E. antarcticus* caused by variation in their three respective significant explanatory variables. Note that in each graph, two of the explanatory variables are held constant while the third varies (see figure caption). The model predicts a strong negative relationship between soil conductivity and the probability of a soil containing viable populations of *S. lindsayae* and *E. antarcticus* (Figs. 5a, 5d). *S. lindsayae* is the more salt tolerant of the two species; the model predicts a higher probability

TABLE 3

Pearson correlation matrix for selected geochemical and biological parameters from Bull Pass for samples containing *S. lindsayae* ($n = 8$).

	Sulfate (ppm)	Chloride (ppm)	Nitrate (ppm)	EC (μS cm^{-1})	pH	Organic Carbon (g kg^{-1})	Total Nitrogen (g kg^{-1})	Soil Moisture (%)	Live Nematodes (log[x + 1])
Sulfate (ppm)	1.00								
Chloride (ppm)	0.98**	1.00							
Nitrate (ppm)	0.98**	0.96**	1.00						
EC (μS cm^{-1})	0.83*	0.78*	0.89**	1.00					
pH	−0.47	−0.37	−0.58	−0.71*	1.00				
Organic Carbon (g kg^{-1})	0.12	0.15	0.15	−0.11	−0.29	1.00			
Total Nitrogen (g kg^{-1})	−0.48	−0.49	−0.40	−0.15	0.13	−0.25	1.00		
Soil Moisture (%)	0.31	0.28	0.42	0.38	−0.30	0.25	0.19	1.00	
Live Nematodes (log[x + 1])	−0.69	−0.56	−0.75*	−0.86**	0.73*	0.19	0.00	−0.42	1.00
Mortality (dead/live)	0.68	0.60	0.77*	0.95**	−0.76*	−0.19	0.06	0.45	−0.95**

*$P < 0.05$; **$P < 0.01$.

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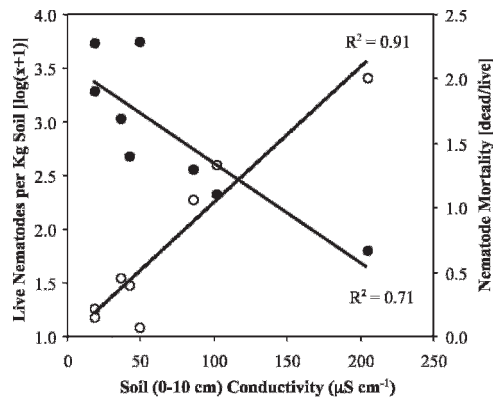
FIGURE 4. Live individuals of *S. lindsayae* per kilogram of soil (solid circles; plotted as log[x + 1]) and *S. lindsayae* mortality (open circles) plotted against soil conductivity. Strong correlations between population parameters and soil conductivity suggest that soil salinity exerts a dominant influence over nematode habitat suitability in Bull Pass soils.

of occurrence compared with *E. antarcticus* over a larger range of conductivities. The model also predicts that the probability of encountering either nematode species is dependent on soil moisture. However, opposite responses are predicted for each species, with the probability of encountering *S. lindsayae* decreasing slightly with increasing soil moisture (Fig. 5b), while that of *E. antarcticus* increased slightly (Fig. 5e). This is consistent with earlier, more localized studies showing a similar difference in response to soil moisture between these two nematode species (Treonis et al., 1999). In addition, the model predicts both a negative relationship between the probability of encountering *S. lindsayae* and total soil nitrogen, as well as a slightly positive relationship between the probability of finding *E. antarcticus* and total organic carbon.

Within the geochemical ranges commonly encountered in the McMurdo Dry Valleys, the effects of soil moisture and total nitrogen on *S. lindsayae* habitat suitability, and the effects of soil moisture and total organic carbon on *E. antarcticus* habitat suitability, are relatively small compared to the effects of soil salinity as measured by conductivity. For example, of the >700 samples compiled for the logistic regression model, 90% of samples with conductivities less than 250 μS cm^{-1}, 56% of samples with conductivities of 250–1000 μS cm^{-1}, and <5% of samples with conductivities greater than 1000 μS cm^{-1} contained live *S. lindsayae* individuals. Within their respective ranges, neither soil moisture, nor total soil nitrogen generated such a striking threshold response with respect to the viability of *S. lindsayae* populations. The pronounced decrease in probability of occurrence with increasing soil conductivity corroborates the Nkem et al. (2006) experiments illustrating similarly steep decreases in nematode survival with increasing salinity.

SPATIAL VARIATION IN HABITAT SUITABILITY

Among the McMurdo Dry Valleys, the high degree of variability in soil salinity generates large variations in nematode habitat suitability. At the regional scale, soil salinity reflects the collective influence of each valley's glacial, hydrologic, and climatic histories (Freckman and Virginia, 1998; Courtright et al., 2001). For example, the higher elevation and colder Beacon and Arena Valleys have high accumulations of soil salts due to long exposure ages (Bockheim, 1997), whereas younger and more hydrologically active areas (i.e. Lake Fryxell and Lake Hoare basins in Taylor Valley) have more dilute soil solute concentrations (e.g. Burkins et al., 2001). There are also smaller-scale variations in soil salinity within each valley reflecting proximity to liquid water such as active streams, lakes, saturated sediments, and snow packs, as well as across prominent landscapes such as patterned ground, hill slopes, topographic depressions, and relict stream channels (Powers et al., 1995; Treonis et al., 1999; Barrett et al., 2002; Gooseff et al., 2003; Moorhead et al., 2003; Barrett et al., 2004; Nkem et al., 2006; MCM-LTER, unpublished data).

Regional variation in soil salt composition may also complicate nematode habitat suitability due to salt-specific effects (Nkem et al., 2006). Keys and Williams (1981) documented regional trends in dry valleys soil salt occurrences related to rock substrate and distance inland from the Ross Sea. Specifically, they showed an increase in the occurrence of nitrate salts and a decrease in the occurrence of chloride salts with increasing distance inland. Similarly, Bockheim (1997) found a transition from chloride- to nitrate-dominated soil salts moving from the coastal regions inland toward the polar plateau. The degree to which these regional trends directly influence habitat suitability is difficult to quantify because large differences in till age within and among the valleys also produce large soil salinity variations. As a consequence, many localities are inhospitable to nematodes irrespective of the specific composition of their soil salts.

Our results demonstrate the extent to which the local scale geochemical variation at Bull Pass provides predictive information about soil factors influencing nematode populations at the regional scale (i.e. the entire dry valleys system). We use the logistic regression model to generate probabilities of *S. lindsayae* occurrence for Bull Pass samples based on measured soil geochemistry (Fig. 6; open circles) and qualitatively compare these probabilities to the observed abundances of *S. lindsayae* (Fig. 6; closed circles). Calculated probabilities of encountering *S. lindsayae* are in excess of 90% in soils between 0 and 900 m along the transect, coincident with a highly suitable habitat for healthy nematode populations (high abundance, high fecundity, and low mortality). Probabilities fall sharply to 0% by 950 m and stay from 0 to 10% from 950 to 1400 m, before rising to 64% between 1400 and 1500 m. No nematodes were found past 900 m, despite the reemergence of more favorable soil conditions, a pattern for which the model cannot account.

TABLE 4

Logistic regression model for occurrence of *S. lindsayae* and *E. antarcticus*.

|	*S. lindsayae* (R^2 = 0.60)					*E. antarcticus* (R^2=0.32)			
Parameter	Slope Parameter β	SE	X^2	p	Parameter	Slope Parameter β	SE	X^2	p
Intercept	2.90	0.22	176.59	0.0001	Intercept	−0.50	0.17	8.62	0.0033
Conductivity	−0.003	0.0003	80.69	0.0001	Conductivity	−0.005	0.0009	32.60	0.0001
Soil Moisture	−0.17	0.04	17.71	0.0001	Soil Moisture	0.12	0.04	7.72	0.0055
Total Soil N	–10.06	4.50	5.02	0.025	Soil Organic C	1.33	0.4776	7.79	0.0052

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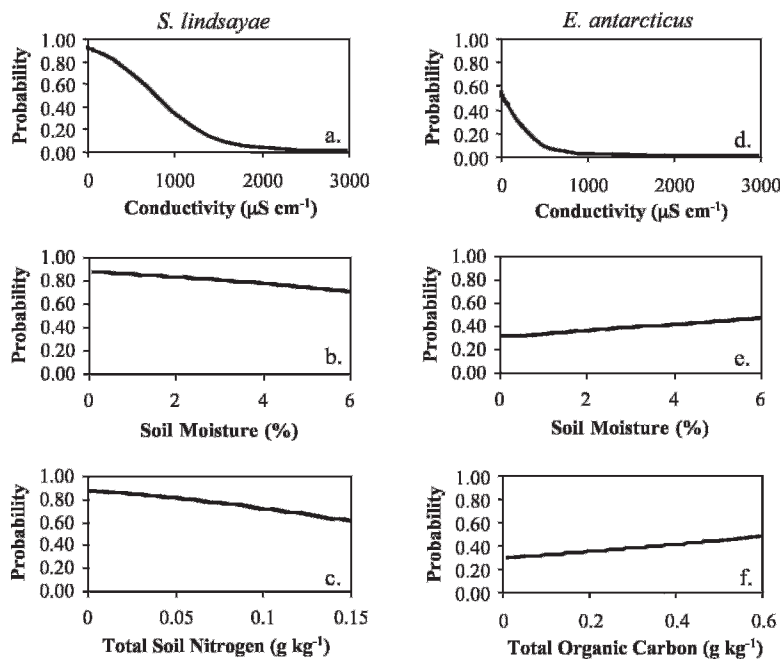
FIGURE 5. Logistic regression model results for *S. lindsayae* and *E. antarcticus* showing the probability of encountering a single live individual plotted against each species' three significant explanatory variables. In each graph, two variables are held constant with the third allowed to vary as plotted. For *S. lindsayae*, conductivity, soil moisture, and total soil nitrogen are held constant at 227 μS cm^{-1}, 1.66%, and 0.03 g kg^{-1}, respectively. These represent the average values for samples where *S. lindsayae* was encountered. For *E. antarcticus*, conductivity, soil moisture, and total organic carbon are held constant at 143 μS cm^{-1}, 2.33%, and 0.3 g kg^{-1}, respectively.

Although the probabilities of *S. lindsayae* occurrence and *S. lindsayae* abundances are not directly comparable, Figure 6 suggests that, at the scale of the Bull Pass transect, the response of *S. lindsayae* communities to variations in soil geochemistry is similar to that of the region as a whole. Similarly, plotting the calculated probabilities of *S. lindsayae* occurrence against measured soil conductivity for all regional samples input into the logistic regression model (Fig. 7; small open circles) as well as for the Bull Pass transect (Fig. 7; large filled circles) shows a similar response among the two sample sets. This suggests that, within the ranges of other soil parameters, salinity exerts a dominant influence over *S. lindsayae* habitat suitability across local to regional scales of variation. The soil geochemistry gradient at Bull Pass may thus provide insights into the delineation of regional geographic distributions of suitable nematode habitats.
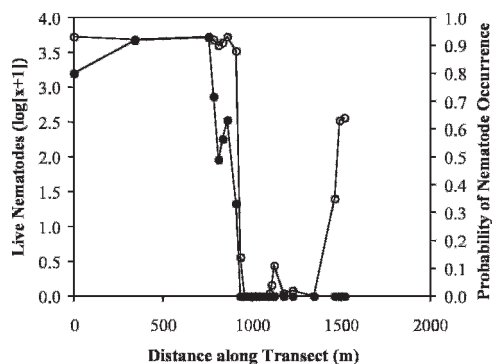
Conclusions

The soil geochemistry at Bull Pass is highly variable along a ~1500 m sample transect exhibiting a range similar in magnitude to that encountered across the dry valleys region. This site provides the opportunity to assess the influence of soil geochemistry on nematode habitat suitability on a local scale, which may be applicable at the regional scale. *S. lindsayae* is the dominant nematode species at Bull Pass with numbers ranging from >5000 live individuals per kilogram of soil to zero in the more saline and inhospitable soils. *S. lindsayae* population numbers and mortality vary systematically across the geochemical gradient correlating most strongly with soil conductivity. A logistic regression model based on soil geochemical properties
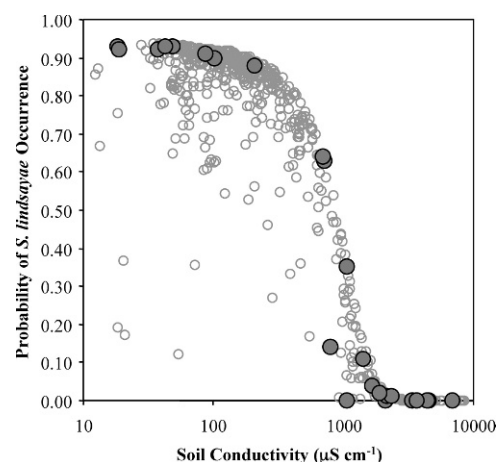

FIGURE 6. Probability of *S. lindsayae* occurrence and live *S. lindsayae* individuals (plotted as log[x + 1]) from the Bull Pass samples plotted against transect distance. Coincident decreases in calculated occurrence probabilities and *S. lindsayae* population numbers suggest that *S. lindsayae* habitat suitability is similarly affected by soil geochemistry at Bull Pass as throughout the larger Dry Valleys ecosystem.

FIGURE 7. Probability of *S. lindsayae* occurrence plotted against soil conductivity from the >700 samples used in the logistic regression model (open circles) showing a steep salinity-driven survival gradient. Data from Bull Pass showing a similar response to soil salinity variation are superimposed on the larger data set (solid circles) and suggest that, within the observed ranges of soil moisture and total soil nitrogen, salinity exerts a first-order control over *S. lindsayae* habitat suitability on both a regional scale between valleys and on a smaller scale within the soil transect at Bull Pass.

and *S. lindsayae* populations from across the dry valleys shows that ~60% of the variability in *S. lindsayae* occurrence can be accounted for by variation in soil moisture, conductivity, and total soil nitrogen, with the most pronounced effect generated by soil conductivity. We suggest that the influence of soil salinity on invertebrate community structure is scale-independent over a range of meters to tens of kilometers and should be considered a primary determining factor explaining nematode habitat suitability.

Acknowledgments

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