

Unique Similarity of Faunal Communities across Aquatic–Terrestrial Interfaces in a Polar Desert Ecosystem

Soil–Sediment Boundaries and Faunal Community

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ABSTRACT

Critical transition zones, such as aquatic–terrestrial interfaces, have been recognized as important features in landscape ecology. Yet changes in the community structure of soil and sediment biota across aquatic–terrestrial boundaries remain relatively unstudied. We investigated the community structure of the dominant fauna, namely nematodes, rotifers and tardigrades, across lake sediment–soil transects in three basins in a species-poor, polar desert ecosystem (McMurdo Dry Valleys, Antarctica). We also examined substrate (that is, soil and sediment) properties, including moisture, salinity, carbon, nitrogen and phosphate concentration, across these transects. Differences in faunal community structure and biochemical properties were typically explained by hydrologic basin and the sediment–soil gradient, but not by transects within each basin. Bonney Basin contained the least organic carbon, chlorophyll *a*, nematodes and taxa, whereas there was little difference in many of these measures between Fryxell and Hoare Basins. Nematode (*Scottinema lindsayae* and *Plectus* sp.) and rotifer abundance varied along sediment–soil transects. *Scottinema lindsayae*, the

most abundant and widely distributed soil animal in this ecosystem, increased in abundance from sediments to soils, whereas *Plectus* sp. and rotifer abundance, and taxa richness (that is, nematodes, rotifers and/or tardigrades), decreased; *Eudorylaimus* sp. and tardigrade abundance did not differ significantly along the transects. Previous studies of soil biodiversity and faunal abundance in this ecosystem have revealed a positive association between these measures and biogeochemistry, if this holds true for lake sediments, our findings suggest sediments in Lake Bonney experience lower rates of nutrient cycling than either Lakes Fryxell or Hoare. Despite differences in faunal abundances along the sediment–soil transects, taxa occurrence was surprisingly similar in soil and sediment, only *S. lindsayae* was restricted to soil or the lake shore. In contrast, in other ecosystems, soil community composition differs greatly from lake sediments, suggesting that the observed similarity in species occurrence in both soils and sediments may be unique to Antarctica. This finding might result from the extreme low diversity of this ecosystem, presumably limiting competition among fauna, and thus promoting broad ecological niches. Alternatively, environmental conditions in Antarctica may select for species with broad ecological niches.

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INTRODUCTION

To date, most ecological studies have focused on either terrestrial or aquatic habitats, with relatively few investigating the interface between these systems. However, there is increasing recognition that more studies examining changes in biological properties and community structure across these boundaries are necessary. This is because these interfaces play a critical role in ecosystem-scale fluxes of water, sediment, energy and nutrients, and these processes are frequently mediated by biota (Wagener and others 1998; Groffman and Bohlen 1999; Bardgett and others 2001; Freckman and others 2001; McClain and others 2003; Wall 2004). The aquatic–terrestrial interface is a major driver of faunal communities in soils and sediments, with many key taxa restricted to one domain or the other, for example, crustaceans, polychaetes, earthworms and collembolans (Wall Freckman and others 1997). Thus, soils and sediments separated by only a few meters typically contain very different biotic communities. Indeed, the differences in community composition represent a major reason why many ecologists limit their area of study to either aquatic or terrestrial ecosystems (Wall and others 2005). As a result, there are few, if any, comparisons in the literature of communities in aquatic sediments with neighboring soils.

Hyper-arid, cold desert ecosystems, such as the McMurdo Dry Valleys of Antarctica (Figure 1), have extremely low levels of faunal biodiversity (Freckman and Virginia 1997, 1998). There are no higher plants, and soil fauna in this region typically consist of up to three taxa (Nematoda, Rotifera and Tardigrada) and only three species of nematodes, making it one of the least diverse terrestrial ecosystems in the world (Freckman and Virginia 1997 1998; Adams and others 2006). This low diversity makes it ideal for determining patterns of abundance and distribution for the entire faunal community, something that is almost impossible in any other ecosystem. Furthermore, and perhaps counter-intuitively, understanding the community structure, composition, and diversity of biota inhabiting substrates (that is, soils and sediments) from species-poor ecosystems may be of greater importance than that of more diverse systems

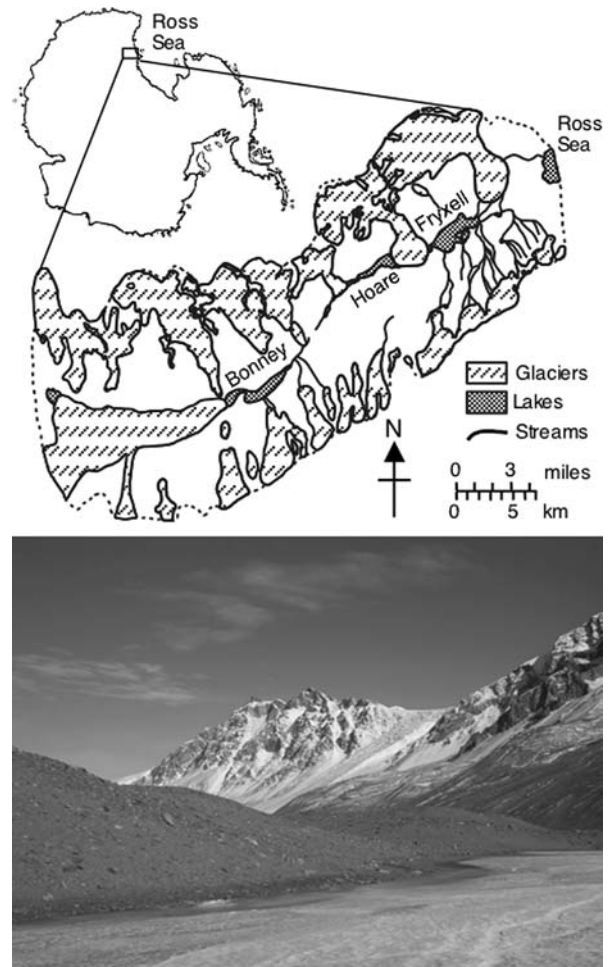


Figure 1. Location of Taylor Valley and the three basins (Fryxell, Hoare and Bonney) studied in this investigation. Photo of Hoare Basin with the frozen surface of Lake Hoare visible (foreground) in the austral summer of 1999–2000.

(Bøhn and Amundsen 2004). This is because experiments examining the relationship between soil species richness and ecosystem processes have only observed strong positive relationships at low levels of biodiversity (<6–10 species), whereas at greater levels of biodiversity which are typical of most soils, the relationship is either weakly positive or neutral (for example, Setälä and McLean 2004; Liiri and others 2002; reviewed by Ayres and others, 2007 in press). Also, in low diversity communities, species traits may be of greater relevance to

ecosystem processes than species richness alone (Heemsbergen and others 2005), indicating that an understanding of community composition is also necessary before links to process rates can be made. As a result, in low diversity ecosystems, differences in biotic community structure across the landscape may relate to larger differences in process rates than would be found in more diverse ecosystems.

Soil faunal communities differ in both richness and composition across the Dry Valleys (Freckman and Virginia 1997, 1998; Barrett and others 2004). Moreover, because the faunal species are known to differ in some traits, they may differentially influence ecosystem processes. For instance, of the three common nematode species, *S. lindsayae* feeds on bacteria and yeast, *Plectus* sp. is a bacterial-feeder and *Eudorylaimus* sp. is an algal-feeder (Overhoff and others 1993; Yeates and others 1993). In addition, *S. lindsayae* has a greater salt tolerance than *Plectus* sp. (Nkem and others 2006). It is likely that the soil fauna exhibit differences in other traits, although this has rarely been investigated. Consequently, there is the potential for differences in community composition and richness across the Dry Valleys landscape to influence process rates in this ecosystem. Indeed, both soil biodiversity and faunal abundance often relate positively to biogeochemistry in this region of Antarctica (Freckman and Virginia 1997, Barrett and others 2004, 2006, 2007, in press). However, without experimental manipulations of species richness and community composition, which have not yet been performed, it is not clear whether this relationship is causative.

In this study, we investigated substrate (that is, soil and sediment) properties, as well as the abundance and distribution of all fauna (nematodes, rotifers and tardigrades), across lake sediment–soil transects in three basins in the Dry Valleys, Antarctica. Nematodes were identified to species, and categorized by sex, age class and living versus dead. This allowed us to determine patterns of faunal community structure and composition across the landscape (that is, between and within basins) and over finer scales across aquatic–terrestrial interfaces. We expected to find distinct faunal communities separated by the aquatic–terrestrial interface and, based on previous studies, we expected Bonney Basin to have lower faunal abundances and diversity than Fryxell or Hoare Basins. Terrestrial ecosystems in Antarctica represent some of the most pristine (that is, least human-disturbed) habitats in the world. As such, they provide a rare opportunity to study patterns of species distribution and ecosystem processes under relatively ‘natural’

conditions. Such data are essential to determine the true magnitude of anthropogenically induced global change on ecosystems. This cannot be easily achieved in many other regions, where historical human influences have already altered the ecosystem.

METHODS

The McMurdo Dry Valleys (Figure 1), southern Victoria Land, contain the largest ice-free area on the Antarctic continent (Fountain and others 1999) and have a cold desert climate (mean annual temperature of -16 to -20°C and <10 cm annual precipitation) (Clow and others 1988; Doran and others 2002a). The Dry Valleys landscape consists of glaciers, large areas of arid soils devoid of vascular plants, permanently ice-covered lakes and ephemeral streams. Taylor Valley (~ 35 km long; 77°S , 162°E) stretches from the Polar Plateau to the Ross Sea, and we sampled the three major hydrological basins along this valley (Fryxell, Hoare and Bonney Basins) (Figure 1). The lakes range in size from 2 (Hoare) to 7 km² (Fryxell) (Spigel and Priscu 1998). The soils of Taylor Valley are typically composed of over 95% sand, with very low concentrations of organic matter (<2 g kg⁻¹) and high concentrations of salts (Campbell and Claridge 1987; Freckman and Virginia 1997). Aquatic sediments in this region generally have greater clay and organic matter content than soils (Barrett and others 2002). The soil fauna typically consists of up to three taxa (Nematoda, Rotifera and Tardigrada) and only three species of nematode are commonly found (*S. lindsayae* Timm, *Eudorylaimus* sp. and *Plectus* sp.; Freckman and Virginia 1997, 1998; Andrassy 1998; Barrett and others 2004). To date, three and seven species of rotifer and tardigrade, respectively, have been found in the soils of Victoria Land, which encompasses the Dry Valleys, although there is uncertainty associated with these numbers (Adams and others 2006). A survey of soils across the Dry Valleys found that only 65% of samples contained any soil fauna, and of these nematodes were the dominant taxa (Freckman and Virginia 1998).

Fryxell and Bonney Basins were sampled on 9 January 2003 and Hoare basin was sampled on 23 January 2003. The only practical way to reach Taylor Valley is via helicopter from McMurdo Station on Ross Island; therefore, the amount of time spent in the field and the quantity of soil collected was limited. At each basin, soil and sediment were collected (~ 5 cm diameter, 4 cm deep) from four points (at a lake depth of about 50 cm, lake shore,

and at 5 and 10 m from the lake shore) along three transects. The lake shore samples were collected precisely at the interface of the water and the soil. Interannual changes in lake levels have been observed (Foreman and others 2004) and lake levels probably vary during the austral summer when glacial melting is greatest. Therefore, if we had collected the samples on a different day it might have been from a slightly different location. One soil/sediment sample was collected using a sterile plastic scoop (~10 cm long and ~4 cm wide; the substrate is too sandy to use a soil corer) for each position along the transect. The transects were spaced approximately 500 m apart within each basin. Soil fauna were extracted from 100 ml soil or sediment using a modified sucrose centrifugal floatation method (Freckman and Virginia 1993). The extracted animals were identified in brightfield with an Olympus CK40 inverted compound microscope. Total nematodes, rotifers and tardigrades were enumerated and abundance was expressed per unit area (m^{-2}). Species and taxa richness was determined for each sample based on counts. Individual nematodes were categorized into demographic group by developmental stage (juvenile or adult), sex and whether they were alive or dead.

Substrate moisture was determined gravimetrically (water mass per unit soil/sediment mass) by drying at 90°C for 48h and all soil chemical concentrations are expressed on an oven dry weight basis. Substrate pH and electrical conductivity (EC) were measured using a glass electrode (Orion, Waltman, Massachusetts, USA) and a conductivity meter (Corning, Corning, New York, USA), respectively. Excess water was drained from the sediment samples and pH and EC were measured using a 1:2 and 1:5 ratio of fresh soil to deionized water, respectively. Substrate samples were air dried, ground in a ball mill and acidified prior to total organic carbon (C) and total nitrogen (N) concentration measurement on a Carlo Erba 1500 elemental analyzer (Carlo Erba, Lakewood, New Jersey, USA). Values of total soil N concentration were not determined for three samples from Hoare Basin and five samples from Bonney Basin because they were below detection limits. Concentrations of NO_3 and NH_4 in 2.0 M KCl extracts were determined on a Lachat Autoanalyzer (Keeney and Nelson 1982). Substrate phosphate was determined on a spectrophotometer (880 nm wavelength) after extraction with 0.5 M NaHCO_3 . Chlorophyll *a* content was only determined for soils at 5 and 10 m from the lake edge, not lake or shore sediments. Soils were processed at very low light concentra-

tions for chlorophyll analysis and prepared using an acetone extraction procedure (Powers and others 1998). Chlorophyll *a* concentration was determined on a Turner model 111 fluorometer (Turner, Palo Alto, California, USA).

Statistical analyses were performed using nested ANOVAs in JMP. The model included basin as a main effect, as well as transect nested within basin and position on soil-sediment transect nested within basin. All abundance data, as well as nematode species richness, taxa (Nematoda, Rotifera and Tardigrada) richness, soil ammonium, nitrate, phosphate, total N, total C and chlorophyll *a*, were $\log_{10}(x + 1)$ transformed to meet assumptions of normality and homogeneity of variance.

RESULTS

Substrate moisture declined sharply with distance from the lakes to around 5% soil moisture 10 m from the lake edge, accounting for 76% of the variance in this measure (Figure 2A, Table 1). Basin and transect also affected moisture content, but accounted for less than 10% of the variance each. Substrate pH was greatest at Fryxell and least at Bonney, but basin accounted for only 10% of the variation (Figure 2B, Table 1), whereas, transect and position along transect each accounted for 35% of the variation in pH. Substrate pH increased from lake sediment to soil at Fryxell and Hoare, but not at Bonney. Electrical conductivity, a measure of salinity, was not significantly influenced by any of the variables in this study (Figure 2C, Table 1). Concentrations of phosphate in the soil and sediment were greatest at Fryxell Basin, but phosphate concentration did not differ along the transects or between transects (Figure 2D, Table 1). Position along transects significantly affected ammonium concentrations with the lowest concentrations occurring at the lake shore and 5 m from the shore (Figure 2E, Table 1). However, the effect appeared to differ between basins; ammonium concentrations declined from sediment to soil at Fryxell and Hoare, but increased at Bonney. Position also affected nitrate concentrations with the greatest concentrations occurring 10 m from the lake edge, but this trend was primarily driven by nitrate concentrations at Bonney, which had the greatest nitrate levels of the three basins (Figure 2F, Table 1). The organic C content of soils and sediments was greatest at Fryxell and least at Bonney (Figure 2G, Table 1). Carbon content decreased from sediment to soil, although this effect was driven by changes in C content at Fryxell and Hoare. Organic C content also varied significantly

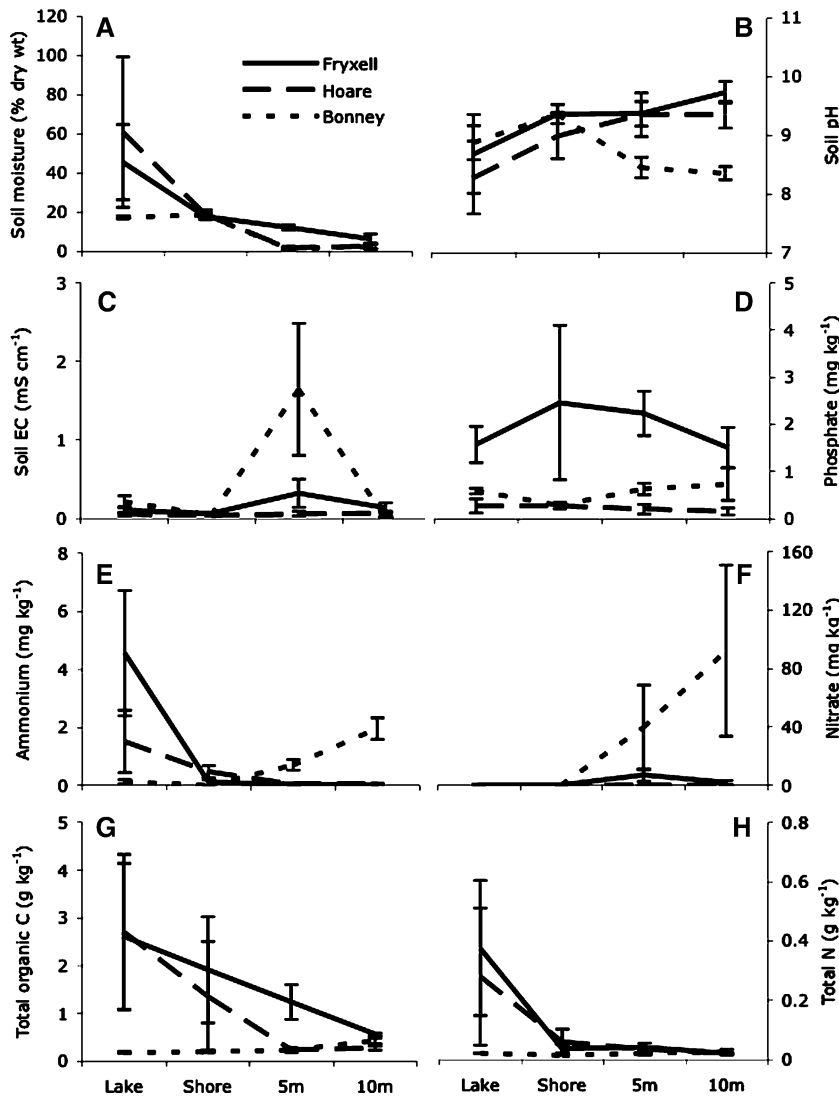


Figure 2. Soil and sediment **A** moisture, **B** pH, **C** electrical conductivity (EC), **D** phosphate, **E** ammonium, **F** nitrate, **G** total organic C and **H** total N along three transects in three basins (Fryxell, Hoare and Bonney). Values are means \pm SE.

between transects. In contrast, total N was not affected by any of the variables measured in this study (Figure 2H, Table 1). Soil chlorophyll *a* concentrations decreased sharply from Fryxell to Bonney Basin; the basin term explained 67% of the variance (Table 2). Transect also significantly influenced chlorophyll *a*, but this measure did not differ between 5 and 10 m from the lake edge (Table 2).

The abundance and distribution of *S. lindsayae* was similar for males, females and juveniles, and for both live and dead individuals (Table 3), therefore, only total abundances are shown (Figure 3). No *S. lindsayae* were observed in Bonney Basin, whereas, they were similarly abundant in Fryxell and Hoare Basins. The abundance of *S. lindsayae* increased with distance from the lake; no individuals were found in the lake sediments, whereas tens of thousands of individuals m⁻² soil

were observed 10 m from the lake shore at Fryxell and Hoare (Figure 3, Table 3). *S. lindsayae* abundance did not vary significantly between transects. The basin and position along transect accounted for the majority of variation of *S. lindsayae* abundance (21–36% and 49–60%, respectively, dependent on age, sex and living versus dead).

As with *S. lindsayae*, the abundance and distribution of *Eudorylaimus* sp. was similar for each age class, sex and living versus dead (Table 3), therefore, only total abundances are shown (Figure 4). *Eudorylaimus* sp. were not observed at Bonney, but were present at Fryxell and Hoare at similar abundances. Thus, there was a significant main effect of basin for all groups of *Eudorylaimus* sp. accounting for 24–41% of the variance (Figure 4, Table 3); dead males and dead juveniles were not analyzed due to their low occurrence. *Eudorylaimus* sp. were present at each position on the transects

Table 1. Effect of Basin, Transect and Position along Transect on Soil/Sediment Measures

	Moisture			pH			EC			Phosphate			Ammonium			Nitrate			Total organic C			Total N			
	df	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P
Basin	2	9	10.4	0.001	10	5.7	0.012	8	1.9	0.186	64	23.2	<0.001	1	0.5	0.628	27	23.1	<0.001	24	10.5	0.001	6	1.4	0.279
Transect (Basin)	6	8	3.0	0.033	36	6.6	<0.001	11	0.8	0.555	7	0.8	0.554	7	1.0	0.432	2	0.5	0.771	28	4.1	0.010	16	1.2	0.363
Position (Basin)	9	76	20.0	<0.001	37	4.5	0.003	44	2.3	0.063	4	0.3	0.946	72	7.1	<0.001	61	11.6	<0.001	27	2.6	0.038	37	1.8	0.140

EC = Electrical conductivity; df = degrees of freedom; %V = variance explained.

from lake sediment to soil. However, neither transect nor position on transect significantly influenced *Eudorylaimus* sp. abundance (Table 3). At Fryxell and Hoare, *Eudorylaimus* sp. were more abundant than *S. lindsayae* in lake sediments, but less abundant in soils.

Every adult individual of *Plectus* sp. was female; males are very rare (Goodey 1963); so this is typical for the species. As with the other nematode species, the abundance and distribution of *Plectus* sp. was similar for each age class, and living versus dead (Table 3); therefore, only total abundances are shown (Figure 5). *Plectus* sp. was the only nematode species found in all three basins, but at Bonney Basin it only occurred at low abundances at the shore (Figure 5, Table 3). Basin accounted for 18–26% of the variance in *Plectus* sp. abundance, dependent on age class and living versus dead. *Plectus* sp. abundance declined from lake sediments to soil 10 m from the lake edge, accounting for 45–66% of the variation. *Plectus* sp. was more abundant than *Eudorylaimus* sp. in sediment, but of similar abundance in soil. Transect significantly affected the total abundance of *Plectus* sp., as well as live females, but only accounted for 8–9% of the variance in this measure.

Nematode species richness was lowest at Bonney, but similar at both Fryxell and Hoare (Figure 6; Table 4), and basin accounted for 68% of the variance in this measure. However, this measure was not affected by the other variables in this study.

Rotifers were found in each basin at similar abundances (Figure 7A, Table 4). Rotifer abundance declined from hundreds of thousands of individuals m^{-2} in lake sediment to around 100 individuals m^{-2} in soils 10 m from the shore, and position along transect accounted for 87% of the variance in this measure. Tardigrades were also found in all three basins, but were only present in lake and shore samples (Figure 7B). However, the variation was great; thus their abundance was not significantly affected by any of the variables (Figure 7B, Table 4).

Taxa richness, that is presence of Nematoda, Rotifera and Tardigrada, was greatest in Fryxell and Hoare Basins (Figure 7C, Table 4). Taxa richness declined from the lake sediment to soil, primarily due to the reduction in rotifers and tardigrades. Basin and position along transect explained similar amounts of the variation in taxa richness, 40 and 46%, respectively.

DISCUSSION

Interfaces between terrestrial and aquatic habitats are of considerable importance to landscape scale

Table 2. Chlorophyll *a* Concentration in Soils 5 and 10 m from the Shore [mean (SE)]

	Chlorophyll <i>a</i> ($\mu\text{g kg}^{-1}$)			Chlorophyll <i>a</i>			
	5 m	10 m		df	%V	<i>F</i>	<i>P</i>
Fryxell	1,358.0 (839.2)	1,357.2 (1,173.2)	Basin	2	67	38.7	<0.001
Hoare	44.9 (30.8)	34.2 (19.8)	Transect (Basin)	6	26	5	0.035
Bonney	8.9 (4.9)	9.5 (4.6)	Position (Basin)	3	1	0.4	0.787

Lake and shore chlorophyll *a* were not measured; *df* = degrees of freedom; %V = variance explained.

processes, such as fluxes of water, sediments, energy, nutrients and organisms (Freckman and others 1997; Groffman and Bohlen 1999; Bardgett and others 2001; McClain and others 2003; Wall 2004). Moreover, organisms that live in soils and sediments mediate these ecosystem processes via individual species/functional group effects, community structure and biodiversity (Wagener and others 1998; Groffman and Bohlen 1999; Bardgett and others 2001; Wall 2004). However, to date, biota in terrestrial and aquatic habitats have usually been studied in isolation from one another. Here we examined changes in substrate properties across lake sediment–soil transects in three basins in a polar desert ecosystem, as well as changes in faunal community structure and biodiversity.

Taken together, basin and distance along transect explained much of the variance in the range of soil physical, chemical and biological properties we measured. In contrast, transect only significantly influenced moisture content, pH and organic C, indicating that at the local scale (~ 0.5 – 1 km) soils and sediments are relatively similar within a basin. Bonney Basin exhibited lower concentrations of chlorophyll *a* and total organic C than Fryxell Basin, but greater concentrations of nitrate; Hoare Basin was typically intermediate reflecting its geographic position in Taylor Valley (Figure 1). Previous studies of soils in the three basins examined here have consistently found lower soil organic matter concentrations at Bonney, which has been attributed to its different climatic and geologic legacies (Barrett and others 2004). Our results extend these findings to lake sediments. Because organic matter content and nutrient availability are important drivers of soil community structure and diversity (Wardle 2002; Bardgett 2005), the differences observed in this study, as well as in previous investigations (Barrett and others 2004; Parsons and others 2004), probably influence the distribution of fauna in this ecosystem.

Position on transect explained the most variation in nitrate and ammonium concentration, 61 and 72%, respectively, similar to previous studies on

ephemeral stream–soil gradients in this region (Barrett and others 2002). Both forms of inorganic N increased from lake sediments to soils in Bonney Basin, whereas, they either decreased or remained unchanged along the transects in Fryxell and Hoare Basins. Although greater concentrations of soil inorganic N typically indicate greater soil fertility, nitrate, which accounted for the majority of inorganic N in Bonney Basin soils, is more toxic than other salts to both *S. lindsayae* and *Plectus* sp., resulting in 100% mortality even at relatively low concentrations (Nkem and others 2006). Similarly, in temperate soils a range of nitrate compounds were shown to be toxic to nematodes (Tenuta and Ferris 2004). Thus, the observed differences in soil properties between basins and along the transects have the potential to influence soil faunal distribution.

Within each nematode species, the abundance of males, females and juveniles as well as living versus dead, varied in a similar pattern between basins and transects, as well as along the transects. Thus, it appears the differences in substrate properties encompassed by this study do not influence nematode population sex ratio, age class or mortality. Similarly, in a study of fauna across soil polygons in Fryxell, Hoare and Bonney Basins, Barrett and others (2004) observed few differences in the ratios of males:females, adults:juveniles and live:dead for *S. lindsayae*, *Eudorylaimus* sp. and *Plectus* sp. between basins. However, there were some differences in these ratios, which appeared to relate to the topography of soil polygons, a common feature of the Dry Valleys (Barrett and others 2004).

At the landscape scale, basin was an important determinant of faunal abundance and diversity, whereas, within each basin, transects located approximately 500 m apart rarely differed in faunal abundance and diversity. Basin typically accounted for 20–40% of the variation in nematode abundance, as well as around 70 and 40% of the variation in nematode species and taxa richness, respectively. Bonney Basin supported smaller populations of *Plectus* sp. than Fryxell and Hoare,

Table 3. Effect of Basin, Transect and Position along Transect on Nematode Abundances

	Total			Male live			Male dead			Female live			Female dead			Juvenile live			Juvenile dead				
	df	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P	%V	F	P	
<i>Scotttnema</i>																							
Basin	2	36	39.3	<0.001	27	12.4	<0.001	21	10.0	0.001	33	29.4	<0.001	33	18.5	<0.001	33	31.1	<0.001	29	29.0	<0.001	
Transect (Basin)	6	3	1.0	0.431	1	0.1	0.995	5	0.8	0.605	2	0.7	0.628	2	0.4	0.845	5	1.5	0.238	2	0.6	0.758	
Position (Basin)	9	53	12.7	<0.001	53	5.4	0.001	56	6.0	<0.001	54	10.7	<0.001	49	6.2	<0.001	53	11.1	<0.001	60	13.4	<0.001	
<i>Eudorylaimus</i>																							
Basin	2	37	7.8	0.004	25	4.3	0.030	-	-	-	26	5.0	0.018	24	4.7	0.023	41	9.9	0.001	-	-	-	
Transect (Basin)	6	10	0.7	0.642	12	0.7	0.657	-	-	-	9	0.6	0.760	7	0.5	0.823	9	0.8	0.616	-	-	-	
Position (Basin)	9	12	0.6	0.819	10	0.4	0.925	-	-	-	18	0.8	0.658	24	1.1	0.439	11	0.6	0.777	-	-	-	
<i>Plectus</i>																							
Basin	2	26	23.6	<0.001	-	-	-	-	-	-	19	23.6	<0.001	18	10.8	<0.001	23	11.0	<0.001	18	8.1	0.003	
Transect (Basin)	6	9	2.7	0.047	-	-	-	-	-	-	8	3.3	0.024	11	2.2	0.094	13	2.0	0.120	11	1.6	0.204	
Position (Basin)	9	54	10.5	<0.001	-	-	-	-	-	-	66	18.2	<0.001	56	7.3	<0.001	45	4.8	0.002	52	5.2	0.002	

The limited number of dead male and juvenile *Eudorylaimus* sp. prevented statistical analysis. Male *Plectus* sp. are very rare in the Dry Valleys and none were found as part of this study; df = degrees of freedom; %V = variance explained.

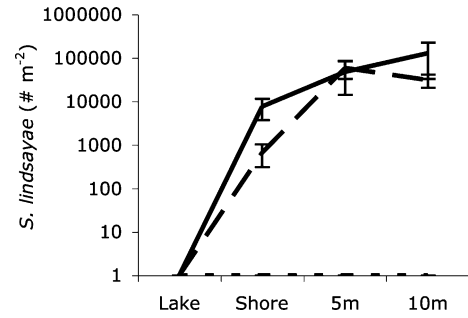


Figure 3. *Scotttnema lindsayae* abundance ($x + 1$) along three transects in three basins. Solid line: Fryxell; dashed line: Hoare; dotted line: Bonney. Values are means \pm SE.

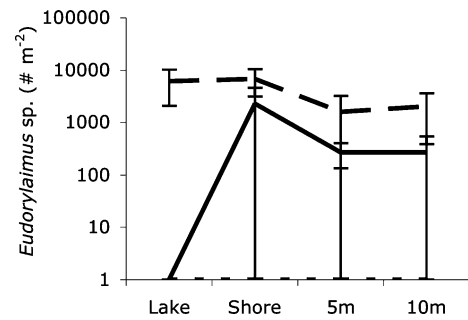


Figure 4. *Eudorylaimus* sp. abundance ($x + 1$) along three transects in three basins. Solid line: Fryxell; dashed line: Hoare; dotted line: Bonney. Values are means \pm SE.

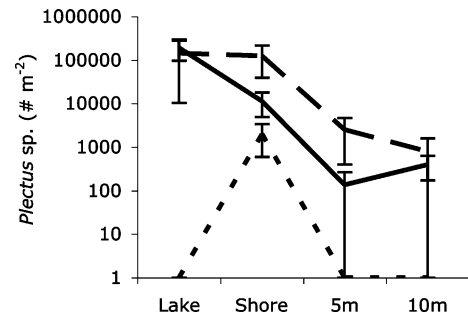


Figure 5. *Plectus* sp. abundance ($x + 1$) along three transects in three basins. Solid line: Fryxell; dashed line: Hoare; dotted line: Bonney. Values are means \pm SE.

and *S. lindsayae* and *Eudorylaimus* sp. were entirely absent from Bonney. Furthermore, Bonney Basin had lower taxa and nematode species richness than both Fryxell and Hoare. Likewise, water from Lake Bonney had lower chlorophyll *a* concentrations, phytoplankton and ciliate biomass, and bacterial production than water from Lake Fryxell, whereas Lake Hoare had intermediate values (Takacs and

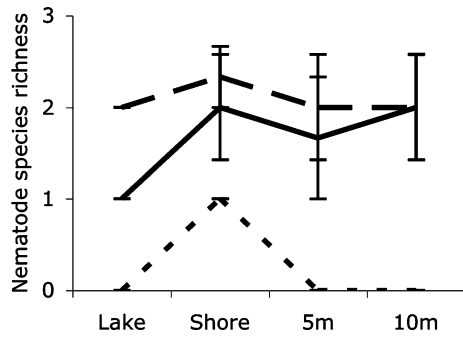


Figure 6. Nematode species richness along three transects in three basins. *Solid line*: Fryxell; *dashed line*: Hoare; *dotted line*: Bonney. Values are means \pm SE.

Priscu 1998; Priscu and others 1999; Roberts and others 2004), suggesting that at the landscape scale, hydrologic basin influences both terrestrial and aquatic organisms similarly. The reduced abundance and diversity of fauna in Bonney Basin may be a result of lower concentrations of organic matter in that basin, as well as greater concentrations of nitrate in the soil. Both *S. lindsayae* and *Plectus* sp. were found to be highly sensitive to potassium nitrate in a lab experiment (Nkem and others 2006), which may explain their absence from Bonney soils. Studies of soils in Fryxell, Hoare and Bonney Basins have observed lower abundance of fauna in Bonney, which was associated with lower concentrations of organic matter and rates of soil respiration, and greater salinity (Barrett and others 2004; Parsons and others 2004). This study provides evidence that sediments in Bonney Basin also support smaller faunal populations and less biological diversity than either Fryxell or Hoare Basins, and this is associated with lower levels of organic matter. Moreover, if the positive relationship between faunal abundance and process rates, which has frequently been observed in soils in this ecosystem (Freckman and Virginia 1997; Barrett and others 2004, 2006, 2007, in press), also occurs in sediments, then our findings suggest sediments in Lake Bonney may have slower rates of nutrient cycling than Lakes Fryxell and Hoare.

The transition from lake sediment to soil was another key determinant of the abundance and diversity of most of the fauna. Position on transect accounted for around 50, 50 and 90% of variation in *S. lindsayae*, *Plectus* sp. and rotifer abundance, respectively, and 50% of variation in taxa richness, suggesting that these measures may be controlled by moisture. *Scottinema lindsayae* was the only faunal group to increase with distance from lake. In contrast, *Plectus* sp. and rotifers declined in abundance

from lake sediment to soil reflecting differences in habitat preferences among these taxa (Treonis and others 1999). Neither *Eudorylaimus* sp. nor tardigrades were significantly influenced by position on transect, although tardigrades were only observed in lake and shore sediments suggesting that they require greater moisture. In terms of abundance, dominance of lake sediment communities followed the sequence rotifers > *Plectus* sp. > tardigrades/*Eudorylaimus* sp., with *S. lindsayae* absent. Whereas, dominance in soils followed the sequence *S. lindsayae* > *Eudorylaimus* sp./*Plectus* sp./rotifers, with tardigrades absent. Treonis and others (1999) observed increased abundance of *S. lindsayae*, and decreased *Eudorylaimus* sp., *Plectus* sp., tardigrade and rotifer abundance, along transects from ephemeral streams to soils in Fryxell Basin. Similarly, other soil studies in the Dry Valleys have shown that *S. lindsayae* typically dominates the soil faunal community in terms of distribution and abundance, whereas *Plectus* sp., *Eudorylaimus* sp., rotifers and tardigrades have much smaller populations and more patchy distributions (Freckman and Virginia 1997, 1998). Interestingly, in soils beyond lake and stream margins the abundance of these faunal groups rarely relates to soil moisture (Freckman and Virginia 1997, 1998; Poage and others 2007, in press), suggesting that moisture is only an important determinant of faunal abundance, community structure and biodiversity at greater levels of moisture found near lakes and streams. It should be noted that lake levels in the three basins are dynamic, for instance the volume of Lake Fryxell decreased by 466,200 m⁻³ between 1991 and 2000 (associated with a reduction in lake level of 5 cm y⁻¹) and an unusually warm 2001–2002 summer increased the volume of Lake Fryxell by 403,300 m⁻³ reversing this trend (Foreman and others 2004). It is not clear how quickly fauna and biochemical properties respond to changes in lake level; therefore, we cannot be certain whether the patterns observed here are a consequence of current conditions or a legacy of prior lake levels.

Although the transition from lake sediment to soil did influence the abundance of much of the fauna, there was surprisingly little change in the occurrence of fauna across this transition zone. *Plectus* sp., *Eudorylaimus* sp., tardigrades and rotifers, common components of the soil faunal community of the Dry Valleys (for example, Freckman and Virginia 1997), were all found in lake sediments, although we cannot be certain that the same species of rotifer and tardigrade occur in both soil and sediment. Moreover, these invertebrates have been found in soils located tens to hundreds of meters

Table 4. Effect of Basin, Transect and Position along Transect on Faunal Abundance and Diversity

	Rotifers				Tardigrades			Nematode richness			Soil taxa richness		
	df	%V	F	P	%V	F	P	%V	F	P	%V	F	P
Basin	2	3	3.5	0.053	3	0.6	0.575	68	44.5	<0.001	40	41.1	<0.001
Transect (Basin)	6	2	0.9	0.542	20	1.2	0.362	2	0.4	0.876	5	1.6	0.212
Position (Basin)	9	87	23.3	<0.001	26	1.0	0.444	16	2.3	0.061	46	10.5	<0.001

Df = degrees of freedom; %V = variance explained; Nematoda, Rotifera, Tardigrada.

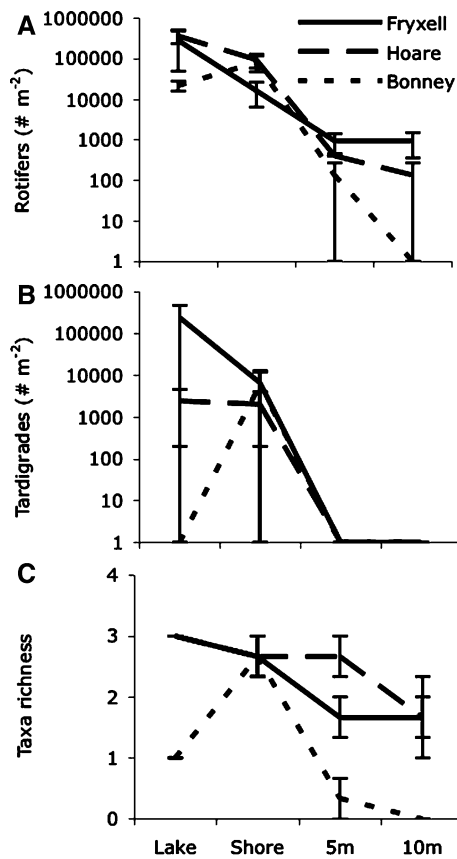


Figure 7. Abundance of **A** rotifers and **B** tardigrades ($x + 1$) and **C** taxa richness (Nematoda, Rotifera and Tardigrada) along three transects in three basins. Values are means \pm SE.

from lakes, albeit often at relatively low abundances (for example, Freckman and Virginia 1997; Powers and others 1998; Barrett and others 2004). *Scottinema lindsayae* was the only invertebrate found that did not occur in lake sediments, although it was found at the lake shore. In contrast, in other ecosystems, sediment and soil communities differ greatly and several taxa are broadly restricted to terrestrial or aquatic environments, for example

crustaceans, polychaetes, earthworms and collembolans (Wall Freckman and others 1997). Indeed, the difference in community composition across the aquatic–terrestrial interface is probably one of the major reasons why ecologists typically restrict their study to only one system rather than both (Wall and others 2005). As a result, there are very few studies that have determined faunal community structure across this transition zone. How can we explain the surprising similarity in faunal community composition across the sediment–soil transition zone in the Dry Valleys of Antarctica? The limited species pool in Antarctica may allow the species present to occupy a broad ecological niche (that is, persisting in soil and sediment), because there are few competitors to exclude them from certain habitats. If this is the case, the introduction of exotic species may substantially alter the structure of these communities, with potential ramifications for ecosystem processes. The presence of root-associated nematodes in regions of Antarctica that are devoid of higher plants suggests that exotic nematodes, and presumably other fauna, are capable of reaching the region (Yeates 1979; Sohlenius and others 2004). Moreover, increased human activity in Antarctica (both scientific and recreational) over recent decades, in tandem with regional climate change (for example, Doran and others 2002b), may have increased the risk of invasion by exotic species (Frenot and others 2005), although this has been poorly studied to date. Alternatively, Antarctica may select for species that are capable of persisting under a wide range of conditions, perhaps as a result of the large annual changes in environmental conditions relative to temperate and tropical regions.

Here we have shown the importance of both spatial scale (that is, between basins) and aquatic–terrestrial boundaries in structuring the faunal community of a cold desert ecosystem. A previous study of faunal distributions across ephemeral stream sediment–soil gradients found little varia-

tion between two sampling points within one summer season (Treonis and others 1999), suggesting that, in the short-term (that is, months), temporal patterns are not important factors for structuring the soil community of the Dry Valleys, whereas, spatial patterns (that is, between basins) and landscape features (that is, lake–soil interface) are more important (Treonis and others 1999; this study). It should be noted, however, that soil faunal populations have been shown to vary considerably over longer time scales of several years (Doran and others 2002b). Other factors associated with soil faunal distribution in the Dry Valleys include elevation, soil polygons, soil pH and salinity (Freckman and Virginia 1997, 1998; Powers and others 1998; Courtright and others 2001; Porazinska and Wall 2002; Barrett and others 2004).

In temperate and tropical ecosystems the biota of soils and sediments mediate process rates, such as water, nutrient and organic matter flux, at the interface between terrestrial and aquatic habitats (Wall Freckman and others 1997; Wagener and others 1998; Groffman and Bohlen 1999; Bardgett and others 2001; Wall 2004). If soil and sediment fauna influence these processes in more extreme environments such as the Antarctic Dry Valleys, the differences in community structure, composition and diversity we have observed between basins may indicate differences in the exchange of matter between terrestrial and aquatic habitats. Indeed, the dissimilarity in faunal communities between basins in the Dry Valleys may have greater consequences for ecosystem processes than differences in community structure found in other ecosystems, which typically contain many more species, trophic groups and taxa. This is because at low levels of soil species richness (<6–10 species), comparable to the Dry Valleys, strong relationships between diversity and ecosystem process rates are often observed, whereas at greater levels of diversity the relationships are weak or not present at all (for example, Setälä and McLean 2004; Liiri and others 2002; reviewed by Ayres and others 2007). However, at low levels of species richness, species-specific traits are probably of greater significance to ecosystem functioning than richness alone (Heemsbergen and others 2004). Although differences in species traits, for example, food source (Overhoff and others 1993; Yeates and others 1993) and salt tolerance (Nkem and others 2006), have been observed for fauna in Dry Valley soils, it is not yet clear if these species differentially affect process rates. Differences in the physical, chemical and biological properties of Lake Fryxell, Hoare and Bonney have been noted (Spigel and Priscu 1998;

Lizotte and Priscu 1998); however, it is not known to what extent, if at all, this relates to their different soil and sediment faunal community and physiochemical properties.

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