

Terrestrial mesofauna in above- and below-ground habitats: Taylor Valley, Antarctica

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Abstract In the McMurdo Dry Valleys region of Antarctica, above-ground production is often limited to mosses and algae that occur near seasonally available liquid water such as ephemeral streams and ice-covered lakes. Compared to surrounding dry soils these critical transition zones are highly productive and harbor a more diverse assemblage of soil animals, including rotifers, tardigrades, nematodes and microarthropods. Current cooling trends punctuated by warming events, and predicted future climate warming are expected to affect the hydrology of this region and thereby biodiversity and ecosystem functioning. Above-ground communities are exposed to more variable temperature, relative humidity and greater UV radiation, and may be more vulnerable to climate change than sediments beneath, which are buffered from short-term changes. In this study, we compared above- and below-

ground communities associated with either moss or cyanobacterial mats along glacial-fed streams and lakes differing in biological complexity (diversity, productivity and habitat suitability). All groups of soil fauna were more abundant in the above-ground material compared to the sediment beneath. Common indicators of habitat suitability (chlorophyll *a*, soil pH, soil salinity, and soil nitrogen) did not differ between vegetation types but were significantly different among sites. Variables most correlated with invertebrate abundances were sediment salinity, chlorophyll *a* content and nitrogen concentration. The McMurdo Dry Valleys are expected to become warmer and wetter as a result of climate change. This will likely increase the area of suitable habitat for most soil animals as areas of liquid water potentially increase and become available for longer periods of time.

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Introduction

In terrestrial environments of the McMurdo Dry Valleys, soils support simple food webs consisting of microbes, protozoa, nematodes, rotifers and tardigrades, with nematodes being the most abundant and widely distributed of the mesofauna (Freckman and Virginia 1998; Adams et al. 2006). Freckman and Virginia (1998) reported that 35% of dry valley soils were devoid of animals and hence were unsuitable habitats; subsequent studies have demonstrated that habitat suitability is a function of local soil properties including availability of soil organic matter and liquid water as well as the deleterious effects of high salinity and

pH (Courtright et al. 2001; Nkem et al. 2006; Poage et al. 2008). Those areas with the highest abundances and diversity of soil animals tend to be in critical transition zones such as aquatic-terrestrial interfaces, and where a distinct habitat gradient occurs between dry soils and wet sediments (Barrett et al. 2002; Treonis et al. 2005; Ayres et al. 2007).

The McMurdo Dry Valleys host no vascular vegetation, but several species of moss, algae and cyanobacteria occur in and near aquatic habitats, such as ephemeral streams, ice-covered ponds and lakes, as well as near snowfields and snow patches (Howard-Williams et al. 1988; Schwarz et al. 1993; Alger et al. 1997; McKnight et al. 1999; Pannewitz et al. 2003). The low biotic diversity and limited carbon inputs in this system result in simple soil food webs dominated by nematodes: the bacterial feeder *Scottinema lindsayae*, the algal-feeder *Eudorylaimus* spp. and the microbial feeder *Plectes* spp. (Adams et al. 2006). In most terrestrial ecosystems, vascular plants greatly influence the distribution and diversity of soil biota, and researchers have reported that above-ground and below-ground communities are linked by feedbacks between production and detrital foodwebs (Wardle et al. 2004; De Dyne et al. 2007). In the McMurdo Dry Valleys little work has focused on relationships between above-ground and below-ground diversity and it is unclear to what extent vegetation (i.e., moss, algae, and cyanobacteria) influences habitat suitability in this environment.

Nematodes, rotifers and tardigrades are known bryofauna (Kinchin 1989), which provide a complex habitat for invertebrates (Overgaard-Nielsen 1948), and have been found in mosses in several areas of continental and maritime Antarctica (Caldwell 1981; Schwarz et al. 1993; Newsham et al. 2004; Dartnall 2005; Sohlenius and Bostrom 2006; Yergeau et al. 2007). Similarly, these animals are known inhabitants of Antarctic microbial (algal and/or cyanobacterial) mats (Yeates 1970; Suren 1990; Andrassy and Gibson 2007). It is expected that these areas of above-ground production will be most affected by climate change due to impacts on water availability and length of the growing season (Wall 2007; Barrett et al. 2008b). Climate variation will also impact soil biota, as pulses of soil moisture and organic matter have been shown to alter soil communities (Burkins et al. 2000; Treonis et al. 2005; Barrett et al. 2008b). Investigating both the above- and below-ground habitats in a simple system such as this can yield information on the linkages between environments, across sites and vegetation types, and how these relationships impact ecosystem function.

In this study, we sampled the above-ground and below-ground community in glacial stream and lake margin environments representing a gradient of primary productivity and habitat suitability. We hypothesized that sites with a more abundant and diverse community of vegetation

(mosses, algae and cyanobacteria) would maintain a more abundant and diverse faunal community both above- and below-ground because of the greater availability of carbon and water. We expected that below-ground habitats would be preferred over above-ground habitats because they are buffered from environmental changes such as fluctuations in temperature, moisture or stream flow, but still subject to above-ground inputs. Since mosses are less abundant than algae and cyanobacteria, and tend to be slow growing and occur in drier areas, we expected soil animals to be more numerous and diverse in habitats associated with microbial mats. Given the potential influence of the biota on nutrient cycling in these highly diverse and productive areas (Schwarz et al. 1993; Bardgett et al. 2001; Barrett et al. 2008a), it is important to understand the relationship between sediments and above-ground vegetation, especially in recognized critical transition zones that may increase in size and importance with climate change in the southern hemisphere.

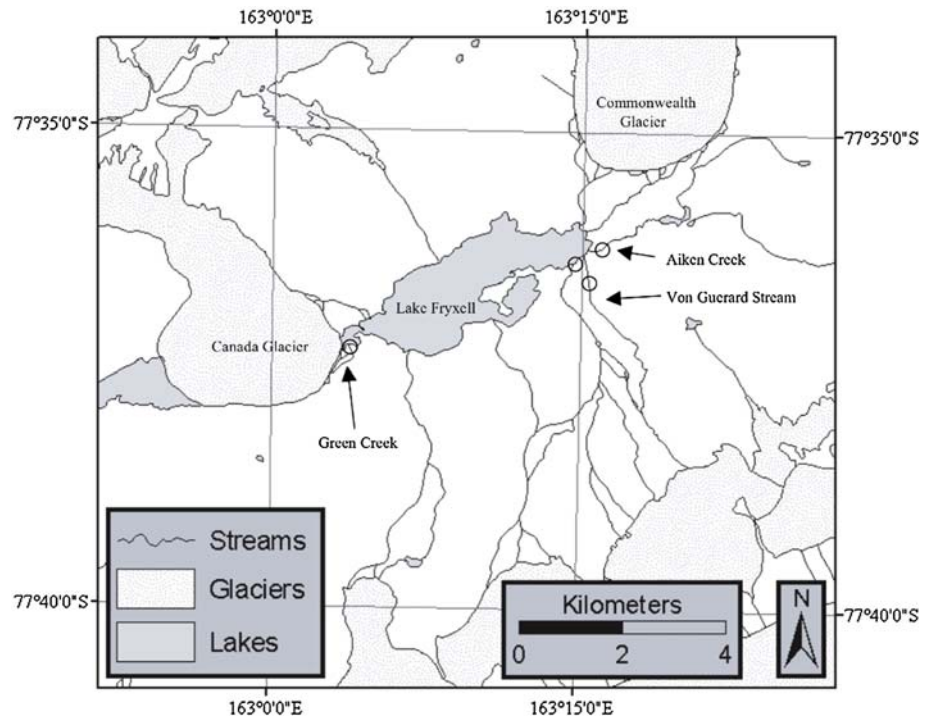
Methods

Study site

This study was conducted in Taylor Valley on the south side of Lake Fryxell basin (77°38'S, 163°06'E) in the McMurdo Dry Valley region of Antarctica (Fig. 1). Average annual temperatures range from -15 to -20°C and precipitation is limited to <100 mm of annual snowfall (Doran et al. 2002). The hyper-arid soils of this region are typically sandy, alkaline and saline (Campbell and Claridge 1987). Carbon and availability of liquid water are the major limiting factors for life in this ecosystem (Kennedy 1993; Barrett et al. 2007). Soil organic matter at low elevations is partially derived from paleo-lake sediments and highly localized areas of contemporary productivity (Burkins et al. 2000; Elberling et al. 2006), and redistribution of these resources is abiotically driven (Hopkins et al. 2006). Sources of liquid water to soil during the austral summer include snow melt (Gooseff et al. 2003), glacial melt-streams, groundwater seeps, permafrost (Lyons et al. 2005; Harris et al. 2007; Barrett et al. 2008a) and wicking of water from the shorelines of lakes and streams through saturated sediments to adjacent soils (Gooseff et al. 2007; Northcott et al. 2009).

Taylor Valley streams are glacier-fed, flowing for up to 10 weeks per year (McKnight et al. 1999). Microbial mats occur in distinct communities spatially delimited by stream channel morphology and flow conditions (Alger et al. 1997). Orange cyanobacteria (*Phormidium* sp., *Oscillatoria* sp.) are found in flowing water in the center of the stream channel, while black cyanobacteria (generally *Nostoc* sp.)

Fig. 1 Map of the Lake Fryxell basin in Taylor Valley, McMurdo Valley region, Antarctica. Sample sites are designated with *open circles*



dominate stream margins (Niyogi et al. 1997; Adams et al. 2006). Microbial mats are desiccation tolerant, capable of surviving long periods of dry conditions, and can rapidly accumulate significant biomass during re-wetting (McKnight et al. 1999, 2007). Variation in primary productivity within and among streams has been attributed to differences in algal and cyanobacterial biomass, diversity, physical structure and duration of submersion in the stream channel (Niyogi et al. 1997). The presence of microbial mats in the streams has a significant effect on nutrient flow from the glaciers into the lakes, where streams with microbial mats contribute fewer nutrients to the lake due to uptake for primary production (McKnight et al. 2004).

There are only eight species of moss known from this area of Antarctica (Seppelt and Green 1998; Adams et al. 2006). Extremely slow growing, Antarctic mosses are desiccation tolerant (Seppelt and Green 1998), adapted to high light intensity (Pannowitz et al. 2003). Unlike microbial mats, moss colonies are not typically present in fast-flowing stream channels, although mosses are often locally abundant on the intermittently saturated sediments adjacent to streams and lakes, and may become submerged during periods of high stream flow (Schwarz et al. 1993; Alger et al. 1997). Two species, *Ceratodon purpureus* and *Bryum argenteum*, are known to have UV-shielding properties (Green et al. 2005). Two other dry valley species, *Sarco-neureum glaciale* and *Bryum pseudotriquetrum*, have been shown to actively retain more precipitation and nitrogen than dry soil (Greenfield 1992).

Sampling

Mosses were collected from soils along Von Guerard Stream, Aiken Creek and Green Creek. Microbial mats were collected from sediments at the edges of Von Guerard Stream, Aiken Creek, Green Creek, and Lake Fryxell. Microbial mats collected from Von Guerard Stream and Lake Fryxell were exposed to the air at the time of collection, while microbial mats from Green and Aiken creeks were submerged. Moss patches were isolated and further from the stream edge than microbial mats, but were within the same general sampling area. These sites were selected because they represented a modest gradient of habitat and primary production; Aiken Creek has lower moss and microbial mat density than is found in Von Guerard Stream, while Green Creek is considered more productive and contains abundant vegetation (Alger et al. 1997). Lake Fryxell is in a closed basin fed by several meltwater streams (Fig. 1), with microbial mats located sporadically on the shoreline and was selected as a contrast.

Five replicate samples were collected for each vegetation type at each stream. Moss or microbial mats were carefully removed from the sediment surface using a spatula and placed in a Whirlpak® bag. A subsample was placed in a 30 ml amber nalgene bottle for analysis of chlorophyll *a*. The sediment beneath the vegetation was sampled to 10 cm (approximately 500 g) using a sterile scoop and placed in a separate, sterile Whirlpak® bag. The shallow rhizoid development allowed collection of the above-ground portion

with minimal disturbance to the below-ground portion. All samples were placed in an insulated ice chest for transport to Crary Laboratory at McMurdo Station.

Mesofauna from both above- and below-ground samples were processed similarly. Sediment and vegetation were sub-sampled under a laminar flow hood using sterile techniques. Nematodes, tardigrades and rotifers were extracted within 48 h from 100 g fresh soil sub-samples that were wet sieved and centrifuged in a sugar solution (Freckman and Virginia 1993). For vegetation, 25 g of fresh mat material and 50 g moss was used for extraction. All fauna were enumerated under an inverted light microscope (100–400 \times), and nematodes identified to genus and classified by sex, life stage (juvenile/adult) and mortality (live/dead). Animal abundance is reported as the number of live organisms per kg dry material. Nematodes were heat fixed in a 4% formalin solution for permanent storage at Colorado State University. Soil moisture content was determined gravimetrically; sub-samples of soil were dried at 105°C for 48 h. Total dry weights of mosses and microbial mats were obtained by drying sub-samples of material at 65°C for 48 h.

Sediment pH was estimated on 1:2 soil extracts using deionized water on an Orion model 720A pH meter (Orion, Waltham, MA, USA). Salinity was estimated by measuring electrical conductivity of 1:5 soil deionized water extracts using a Yellow Springs Instrument 3100 conductivity meter (Yellow Springs Instrument Co., Yellow Springs, OH, USA). Sediments were processed and prepared for chlorophyll *a* analysis, a proxy for algal productivity, under low light conditions using an acetone extraction procedure (Powers et al. 1995). Chlorophyll *a* concentrations were measured on a Turner model 111 fluorometer (Turner, Palo Alto, CA, USA). Approximately 20 g of the fine earth fraction was extracted for inorganic N in 50 ml of 2 M KCl. Extracts were shaken for 30 min at 250 rpm and centrifuged at 15,000 rpm (27,216g) for 10 min on a Beckman Coulter centrifuge (Model Aranti J-20XPI) to settle suspended matter. The supernatant was decanted and frozen prior to analysis on the Crary Laboratory Lachat Autoanalyzer. Soil organic C (SOC) content was determined on dried, ground, and acidified sub-samples with a EA 1112 CHN analyzer (CE Elantech, Lakewood, NJ, USA) at Virginia Polytechnic Institute and State University.

Analysis

ANOVA was used to determine differences among sites and between vegetation types (microbial mats and moss) and habitat (above or below) using the fit model procedure in JMP 5.0. (SAS Institute Inc.) The variable “vegetation type” was nested within “site” because not all sites contained both vegetation types. If appropriate, post hoc

Tukey’s HSD test followed the ANOVA. Population data were calculated on a dry weight basis and transformed (\log_{n+1}) to fit assumptions of normality. Sex ratio (number of living males per living female), number of living juveniles per living female, and number of dead individuals per living individuals) were calculated for *Eudorylaimus* spp. and *Plectus* spp. only. Sex ratio was not calculated for *Plectus* spp. because no males were found at these sites. These life cycle parameters were not transformed for analysis. Simple regression analysis was performed to investigate possible relationships between above- and below-ground faunal communities. Where possible, correlation analyses were used to assess relationships between invertebrates, soil moisture, chlorophyll *a*, and soil chemical variables. Differences were considered significant at $P \leq 0.05$.

Results

All known groups of terrestrial mesofauna described from the McMurdo Dry Valleys were extracted from samples in this study, including four nematode species (Table 1). Species richness was highest at Lake Fryxell and Aiken Creek due to the presence of a single *Scottinema lindsayae* at each site, but no other individuals of this species were found. Several morphotypes of Rotifera and Tardigrada were noted, but not differentiated for this study. *Eudorylaimus* spp. was most abundant at Green Creek, and least abundant at Lake Fryxell. In contrast, *Plectus* spp. were found in the highest numbers at Lake Fryxell. Rotifers and tardigrades were also abundant at Lake Fryxell but found in the highest densities at Green Creek. *Plectus* spp., rotifers and tardigrades were more abundant in algae compared to moss, while *Eudorylaimus* spp. was not affected by vegetation type (Table 2). *Eudorylaimus* spp., *Plectus* spp., rotifers and tardigrades were all more abundant in above-ground vegetation compared to the sediment directly below (Table 1).

While sex ratio of *Eudorylaimus* spp. did not differ among sites or between habitat or vegetation types, the number of juveniles per female was highest at Von Guerard Stream and lowest at Lake Fryxell (site, $P = 0.03$), and higher in sediment compared to above-ground vegetation ($P = 0.03$). Mortality (dead: living) of *Eudorylaimus* spp. also varied with site ($P = 0.03$) and habitat ($P = 0.01$). Dead juveniles were more abundant below-ground ($P = 0.01$). Neither number of juveniles per female or mortality of *Plectus* spp. were affected by site, vegetation type or habitat.

Abundances of *Plectus* spp. in above-ground and below-ground habitats were positively correlated in both microbial mats ($r^2 = 0.56$, $P = 0.01$) and in moss communities ($r^2 = 0.39$, $P = 0.01$). In contrast, abundances of *Eudorylaimus* spp. in the above-ground and below-ground habitats

Table 1 Soil animal abundances in above-ground and below-ground samples at four sites for two vegetation types (microbial mat and moss) in Taylor Valley, Antarctica

Site	Vegetation	Habitat	Nematoda			Rotifera	Tardigrada
			<i>n</i>	<i>Eudorylaimus</i> spp.	<i>Plectus</i> spp.		
Aiken Cr	Microbial mat	Above	5	0.45 ± 0.22 ab	9.08 ± 3.75 b	87.44 ± 26.00 ab	139.29 ± 49.43 a
		Below	5	0.36 ± 0.15 ab	0.12 ± 0.03 d	0.33 ± 0.19 e	0.32 ± 0.07 e
Green Cr	Microbial mat	Above	5	1.08 ± 0.53 ab	59.05 ± 23.59 a	210.60 ± 148.58 a	145.07 ± 95.70 a
		Below	5	0.57 ± 0.13 ab	0.33 ± 0.09 d	0.29 ± 0.06 e	0.91 ± 0.10 de
Lk Fryxell	Microbial mat	Above	5	0.06 ± 0.06 b	118.71 ± 38.12 a	183.58 ± 32.18 a	110.90 ± 26.24b
		Below	5	0.12 ± 0.05 b	2.63 ± 0.99 bcd	8.47 ± 3.54 cde	2.78 ± 0.98 cde
Von Guerard Str	Microbial mat	Above	5	1.17 ± 0.86 ab	5.58 ± 1.19 bc	28.01 ± 8.86 bc	16.91 ± 6.08 bcd
		Below	5	0.37 ± 0.23 ab	0.86 ± 0.22 d	2.93 ± 0.88 de	1.67 ± 0.85 de
Aiken Cr	Moss	Above	5	0.94 ± 0.20 ab	1.15 ± 0.29 cd	1.36 ± 0.51 e	1.75 ± 0.98 de
		Below	5	0.69 ± 0.27 ab	0.55 ± 0.19 d	0.18 ± 0.08 e	0.63 ± 0.38 e
Green Cr	Moss	Above	5	1.92 ± 0.85 a	8.04 ± 1.97 b	22.85 ± 9.87 bcd	16.41 ± 2.49 abc
		Below	5	0.46 ± 0.08 ab	0.83 ± 0.33 d	1.56 ± 0.73 e	0.75 ± 0.08 de
Von Guerard Str	Moss	Above	5	1.09 ± 0.23 ab	2.26 ± 0.36 bcd	43.37 ± 21.21 bc	1.22 ± 0.35 de
		Below	5	0.21 ± 0.07 ab	0.30 ± 0.15 d	4.15 ± 3.41 e	0.01 ± 0.00 e

Data represent mean number of viable individuals (±SE) in a gram of dried material; different letters represent post hoc Tukey's test for significant differences among all variables at $P < 0.05$; Cr creek, Lk lake, Str stream

Table 2 *F* values for analysis of variance

	Nematoda		Rotifera	Tardigrada
	<i>Eudorylaimus</i> spp.	<i>Plectus</i> spp.		
Site	4.31*	44.28***	15.54***	12.70***
Vegetation [site]	1.08	6.29***	7.55**	11.84***
Habitat	4.98*	258.71***	158.21***	129.80***
Site*Habitat	1.31	18.43***	1.53	4.86*
Vegetation*Habitat	0.75	10.15***	8.49***	9.62***

The variable "vegetation" (microbial mat, moss) was nested within site, because not every site contained both types of vegetation
Significant differences are noted with asterisks: * $P \leq 0.05$; ** $P \leq 0.001$; *** $P \leq 0.0001$

were not correlated in either vegetation type (microbial mats: $r^2 = 0.07$, $P = 0.25$; and moss: $r^2 = 0.06$, $P = 0.36$). Abundances of rotifers collected above-ground were not correlated with abundances below-ground in either microbial mats ($r^2 = 0.03$, $P = 0.49$) or moss ($r^2 = 0.14$, $P = 0.17$). This was also true of tardigrades (microbial mats, $r^2 = 0.01$, $P = 0.87$; moss, $r^2 = 0.22$, $P = 0.08$).

Chlorophyll *a* content of vegetation varied by site ($P = 0.01$, Fig. 2a), but there were no differences between the vegetation types ($P = 0.38$). Sediment pH was higher at Aiken Creek ($P < 0.0001$; Fig. 2b) but was similar between vegetation types ($P = 0.44$). Electrical conductivity (EC) was higher at Lake Fryxell ($P < 0.0001$; Fig. 2c) than in sediments collected from other sites, but did not vary by vegetation type ($P = 0.22$). Sediments from beneath microbial mats at Lake Fryxell were lowest in NO_3^- ($P = 0.15$; Fig. 3a) and highest in NH_4^+ concentration

($P = 0.01$) compared to other sites. For this reason, dissolved inorganic nitrogen (DIN) was higher at Lake Fryxell as well ($P = 0.02$; Fig. 3b). All samples were moist to saturated, but moisture content was highest in the microbial mats at Aiken Creek ($P < 0.0001$). Sediment organic C content ranged from 1.63 to 31.77 mg/L but did not differ among sites ($P = 0.08$) or between vegetation types ($P = 0.48$).

Correlation coefficients between soil animal abundances and soil variables are shown in Table 3. *Eudorylaimus* spp. abundances were not significantly correlated with any other invertebrates or environmental variable. *Plectus* spp. were positively correlated with rotifers, tardigrades, ammonium, total inorganic nitrogen, chlorophyll *a* and salinity. Rotifers and tardigrade abundances were positively correlated with each other as well as *Plectus* spp., sediment nitrogen, chlorophyll *a*, moisture, and salinity, but negatively correlated

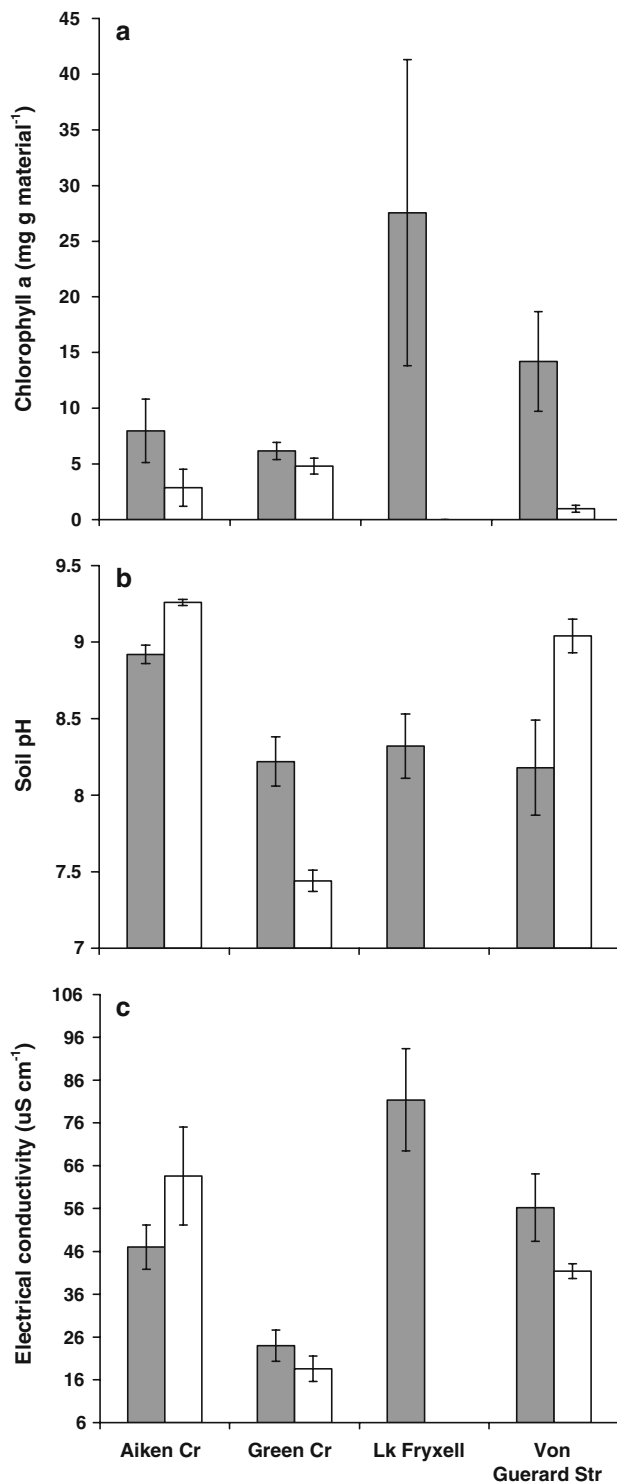


Fig. 2 Mean (\pm SE) habitat parameters **a** chlorophyll *a* concentration, **b** sediment pH, and **c** sediment electrical conductivity from samples taken at four aquatic-terrestrial transition zones in Taylor Valley, Antarctica. Shaded bars represent samples collected from moss colonies, open bars represent samples take from algal mats

with sediment pH (Table 3). Tardigrades were also negatively correlated with sediment pH. There were no significant relationships between any fauna and organic C

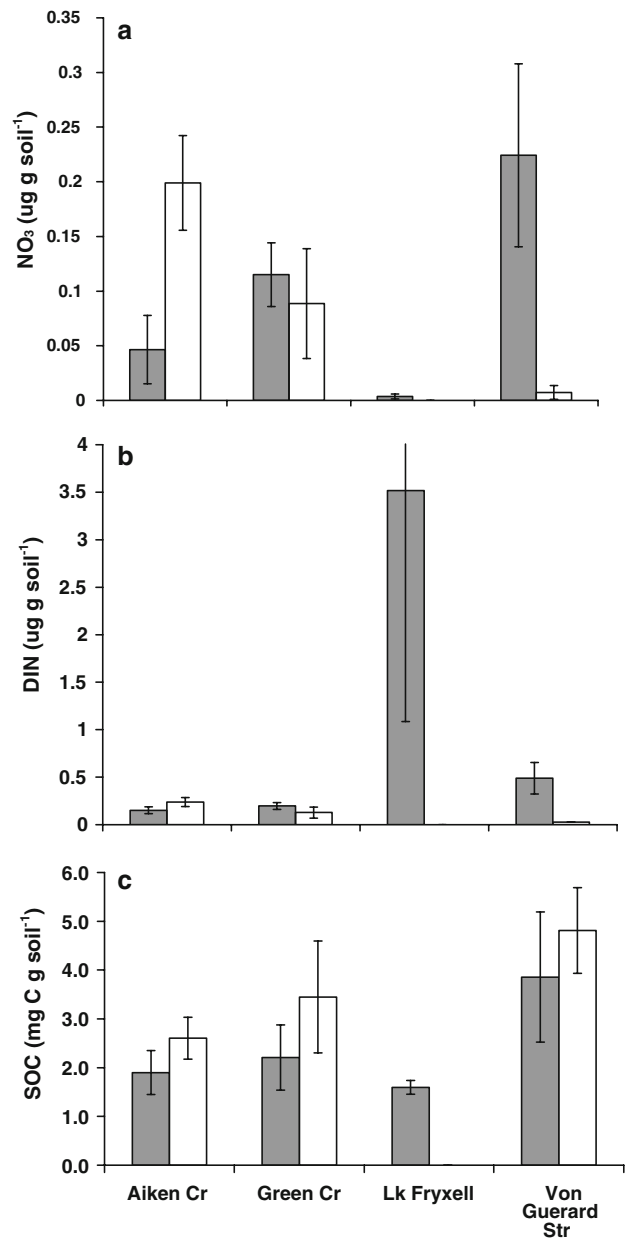


Fig. 3 Mean (\pm SE) KCl-extractable **a** NO₃⁻, **b** total dissolved nitrogen, and **c** Organic C content from sediment samples taken at four aquatic-terrestrial transition zones in Taylor Valley, Antarctica. Shaded bars represent samples collected from moss colonies, open bars represent samples take from algal mats. Upper limit standard error bars for Lk Fryxell in B were removed for clarity

content, therefore it is not included in the correlation matrix.

Discussion

In this study, we characterized the above-ground and below-ground faunal community associated with vegetated areas across several sites of varying habitat suitability in

Table 3 Correlation matrix of viable invertebrate abundance (\log_{10+1}) per gram of dry material and environmental variables at four sites in Taylor Valley, Antarctica

Parameter	Nematoda		Rotifera	Tardigrada
	<i>Eudorylaimus</i> spp.	<i>Plectus</i> spp.		
<i>Eudorylaimus</i> spp.	1.00	−0.15	−0.26	−0.10
<i>Plectus</i> spp.	−0.15	1.00	0.77***	0.79***
Rotifera	−0.26	0.77***	1.00	0.60***
Tardigrada	−0.10	0.79***	0.60***	1.00
NO ₃	0.10	−0.07	−0.29	−0.03
NH ₄	−0.16	0.49*	0.46*	0.59*
DIN	−0.15	0.49*	0.45*	0.59*
CHL A	−0.25	0.72*	0.50*	0.63*
H ₂ O	−0.30	−0.17	0.16	−0.35
pH	0.07	−0.29	−0.29	−0.58*
EC	−0.37	0.63*	0.38	0.41*

Chlorophyll *a* measurements from vegetation only ($n = 35$); moisture from vegetation and soil ($n = 70$); all other measurements from sediment only ($n = 35$)

Abbreviations are as follows: NO₃, sediment nitrate concentrations ($\mu\text{g/g}$ soil); NH₄, sediment ammonium concentrations ($\mu\text{g/g}$ soil); DIN, total dissolved nitrogen concentration ($\mu\text{g/g}$ soil); CHL A, chlorophyll *a* concentrations (mg/g dry material); H₂O, moisture content (g/g soil); EC, electrical conductivity ($\mu\text{S/cm}$)

Significant differences are noted with asterisks: * $P \leq 0.05$; ** $P \leq 0.001$; *** $P \leq 0.0001$

Taylor Valley, Antarctica. We have shown that when vegetation is present in critical transition zones, such as aquatic terrestrial interfaces, soil-dwelling animals are more abundant in above-ground compared to below-ground habitats. Numerous studies have shown that inputs from the above-ground plant community significantly impact below-ground faunal community structure, and these soil communities in turn are responsible for both positive and negative feedbacks to the plant, both directly and indirectly (Wardle et al. 2004). The activity of above-ground plant-associates has also been shown to affect the below-ground community, and vice versa (De Dyne et al. 2007). Furthermore, soil biota in these critical transition zones influence nutrient transfer in hydrological pathways, ultimately affecting biogeochemical processes, both aquatic and terrestrial (Bardgett et al. 2001).

The soils of the McMurdo Dry Valleys are characterized by high spatial heterogeneity (Freckman and Virginia 1998) and extensive areas of low organic matter, low soil moisture and moderate to high salinity, which results in unsuitable soil habitats that are associated with low invertebrate diversity (Burkins et al. 2000; Courtright et al. 2001). Results from this study confirm that, with the exception of *Scottinema lindsayae*, invertebrates in the McMurdo Dry Valleys are more abundant in aquatic sediments compared to dry soils. Habitat suitability changes in aquatic sediments, where seasonal moisture inputs and highly variable nutrient and salinity levels along with the presence of microbial mats or moss are accompanied by a dramatic

increase in invertebrate abundance. Our results are similar to those of Suren (1990) on benthic cyanobacterial mats in ponds at Bratina Island (75 km southeast of Taylor Valley), who reported that sediments contained low densities of invertebrates compared to overlying algal mats.

Although sediments are buffered from extreme variations in climate (Ikard et al. 2009), living in an above-ground habitat may convey advantages to Antarctic mesofauna, especially when the vegetation is adjacent to or in aquatic environments such as lakes and streams. Taylor Valley streams have higher NPP and contain more diverse microbial communities compared to dry soils (McKnight et al. 1999). In alpine streams of New Zealand, Suren (1991) found that mosses reduced water velocity and accumulated large quantities of detritus, which led to greater abundances of invertebrates in the vegetation compared to nearby gravel habitats. Similarly, diatoms, algae, and detritus often found on mosses associated with Taylor Valley streams would serve as a complex food source for sediment invertebrates.

In other systems, the three distinct layers of a moss cushion (canopy, stem, and rhizoid) have been shown to harbor distinct communities of nematodes (Overgaard-Nielsen 1948). Summarized by Kinchin (1989), some nematode genera, such as *Plectus*, migrate through the layers and are early colonizers of young moss patches, while others, such as *Dorylaimus*, are only found in the rhizoid layer of older moss patches. In our study, a significant relationship between above-ground and below-ground populations in

microbial mats and moss patches illustrates that high numbers of *Plectus* spp. in the above-ground vegetation is a good predictor of populations in the sediment beneath. The migratory nature of this genus within moss (Overgaard-Nielsen 1948; Kinchin 1989) means that *Plectus* spp. may be able to take advantage of both above-ground and below-ground habitats in a highly suitable location or patch, which can be beneficial under extreme climatic conditions. Other invertebrates did not display a linear relationship between above- and below-ground habitats, indicating a strong preference for living in the vegetation.

Our results suggest that availability of organic matter is an important component of habitat suitability. Aquatic sediments colonized by cyanobacteria and mosses constitute hot spots of diversity and production in the McMurdo Dry Valleys (Treonis et al. 2005; Hopkins et al. 2006), associated with high turnover rates of soil organic carbon compared to dry soils (Eberling et al. 2006). While there are significantly fewer nematode species present in these cold desert soils, abundances within vegetated “hot spots” are comparable to those found in more temperate environments (Wall and Vignia 1999). Nematodes are known to have a significant effect on nutrient cycling in the low diversity soils of the McMurdo Dry Valleys (Barrett et al. 2008a), as they do elsewhere (Wardle et al. 2004). Therefore, in areas of substantial productivity such as microbial mats and moss patches associated with critical transition zones, high densities of invertebrates likely have a significant impact on both aquatic and terrestrial ecosystem function.

Variables consistently associated with most invertebrate abundances were chlorophyll *a* concentration, sediment salinity, and sediment nitrogen. Chlorophyll *a* concentration has previously been linked to invertebrate populations (Sinclair and Sjørnsen 2001; Treonis et al. 2005), specifically *Eudorylaimus* spp., which is an algal feeder (Wall 2007). In this study, *Eudorylaimus* spp. was not correlated with chlorophyll *a* concentration. However, because the samples were taken from highly productive sites, it is possible that this variable is not as important for predicting biodiversity as it is in dry soils, where microbial biomass is much lower and where organic matter sources are limited to legacy carbon sources and micro-algae (Burkins et al. 2000). This would also explain the lack of relationship between mesofauna and sediment organic C content, which is much higher in sediments compared to surrounding dry soils (Barrett et al. 2007). All other animals were positively correlated with chlorophyll *a* concentrations, indicating that this is a good predictor of habitat suitability for many invertebrates.

In dry soils, where concentrations of salts can be high, animal populations are negatively correlated with salinity (Courtright et al. 2001; Nkem et al. 2006; Poage et al. 2008). In aquatic sediments, where levels of salinity covary with water and organic matter availability, the opposite

may be true. For example, abundances of the effectively aquatic taxa (those typically not found outside of intermittently saturated sediments) *Plectus* spp., rotifers and tardigrades all correlated positively to sediment salinity, ammonium concentrations and total dissolved inorganic nitrogen. The change in the direction of the relationship between invertebrates and salinity in soils and sediments is an example of how habitat suitability characteristics can differ across the landscape; a single predictive model for invertebrate distribution may identify aquatic sediments as more suitable than dry soils, but not be able to properly differentiate within sediments because the range of variation in salinity is much greater in dry soils. *Eudorylaimus* spp. was the only invertebrate to show a negative relationship with salinity and ammonium concentrations in aquatic sediments. Frequent wetting and drying of vegetation, such as the microbial mats at Lake Fryxell and Von Guerard Stream, or moss patches at Aiken Creek, where *Eudorylaimus* spp. was less abundant, would increase salinity due to evaporation (Gooseff et al. 2007; Northcott et al. 2009). Mats associated with Lake Fryxell might be dominated by ammonium because of excessive nutrient uptake by microbial mats in streams, which leads to a reduction in nitrate transport to the lake (McKnight et al. 2004).

The abrupt transition in the mesofaunal community associated with moisture and salinity gradients means that in a warmer, wetter Antarctica, the amount of vegetated areas will increase the suitable habitat for most invertebrates in critical transitional zones. This climate change scenario may support the expansion of *Eudorylaimus* spp. (e.g. Barrett et al. 2008b) and *Plectus* spp. and possibly invasions by opportunistic, cosmopolitan species, at the expense of the dominant, widely distributed endemic nematode *S. lindsayae*, for which such ostensibly rich habitats are unsuitable. In contrast, while endemic Antarctic diatoms responded favorably to decreased stream flow resulting from regional cooling (Esposito et al. 2006), a decrease in available liquid water will limit colonization of wet sediments by vegetation, limiting the amount of suitable habitat for most invertebrates, and potentially favoring increased abundances of *S. lindsayae* in the evaporative zones (Treonis et al. 2005). Currently there is good information on the relationship between algae and nutrient cycling in Antarctic streams (Alger et al. 1997; McKnight et al. 2004). However, we have no information on the relationship between invertebrates and stream variables such as moss cover, microbial species, dimensions of wetted zone, temperature, or nutrient flow. With further study in these areas, it may be possible to link stream dynamics and function with invertebrate populations and life strategies, revealing relationships between animals and their suitable habitats, as well as allowing for better prediction of invertebrate response to environmental change in critical transition zones.

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