DISSERTATION

TROPHIC RELATIONSHIPS IN SOIL COMMUNITIES: HOW ABIOTIC STRESS AFFECTS BIOTIC INTERACTIONS IN THE MCMURDO DRY VALLEYS, ANTARCTICA

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ABSTRACT

TROPHIC RELATIONSHIPS IN SOIL COMMUNITIES: HOW ABIOTIC STRESS AFFECTS BIOTIC INTERACTIONS IN THE MCMURDO DRY VALLEYS, ANTARCTICA

Understanding of the distribution and complexity of soil food webs and their role in ecosystem processes is limited. This is partially due to the difficulty studying the enormous diversity of species in belowground ecosystems and identifying the many roles of this diversity in ecosystem processes. Despite this, there is strong interest in understanding how the soil food web contributes to ecosystem processes such as decomposition, nutrient cycling, and carbon cycling. Yet, before we can fully understand how soil food webs are linked to ecosystem processes, more information is needed on their complex trophic interactions and how soil food webs respond to changing environmental variables. The McMurdo Dry Valleys in Antarctica provide an excellent opportunity to study soil communities and their trophic interactions because of soil food web simplicity and limited ecological interactions that are not easily distinguished in more diverse systems. However, it is unknown whether trophic interactions actually play a role in structuring soil communities in this ecosystem and whether these interactions are affected by environmental factors. The aim of this dissertation is to disentangle those questions.

In the first chapter of this dissertation, I give the background for my research. I introduce the challenges for studying soil biodiversity and its food web structure. Next, I discuss the usefulness of the McMurdo Dry Valleys as a simple, model system for researching trophic interactions in soil. The details of the current understanding of the McMurdo Dry Valley soil food web are demonstrated and I have highlighted gaps in this knowledge. In the second chapter

of this dissertation, I address the question: What trophic interactions are present in the McMurdo Dry Valley soils? Here, I sought to elucidate the soil food web structure using stable isotopes (particularly ^{15}N) and I present isotopic signatures for soil fauna taxa for one location in Taylor Valley, Antarctica. The natural abundance of ^{13}C and ^{15}N were measured for soil fauna and microbial mats sampled in both wet and dry soils near Von Guerard stream. This study revealed that three trophic levels were present in wet soils at this location and two trophic levels were present in dry soil. This is the first isotopic confirmation of *Eudorylaimus antarcticus* (Nematoda) as an omnivore-predator (in wet soil habitat), and challenges long-held assumptions of trophic simplicity of the McMurdo Dry Valley region.

Building on the findings of Chapter 2, Chapter 3 seeks to expand the understanding of dry valley food webs and the role of trophic interactions in structuring communities under environmental change. Specifically, I address the question: How do environmental variables (soil salinity and moisture) affect dry valley soil taxa and their trophic interactions? I show the results of a laboratory microcosm experiment on how elevated salinity and moisture affect four soil communities. Using soil collected from Taylor Valley, Antarctica, bacteria, bacteria with *Scottnema lindsayae*, bacteria with *E. antarcticus*, and bacteria with both *S. lindsayae* and *E. antarcticus* were established in microcosms under control or high salinity treatments and control or high moisture treatments (full factorial design). The results of this experiment showed that *S. lindsayae* has top down effects on bacterial abundance under control salinity but these top down effects were alleviated under high salinity. This study is the first to empirically show that biological interactions structure dry valley soil communities.

The fourth chapter follows the conclusions of Chapters 2 and 3, and seeks to determine food web structure and trophic interactions at the landscape scale in the McMurdo Dry Valleys. I

sampled soil from 160 sites across 8 valleys ranging from the coast to high elevation near the polar plateau to address the question: How does the soil food web and its organic carbon sources vary across the McMurdo Dry Valley landscape with distance from coast and elevation? These valleys represent a temperature and moisture gradient, which affects ecosystem primary productivity. This study revealed that food web structure varies by habitat – the most diverse and complex trophic interactions exist in wet habitat near the coast where resources are more abundant. However, in dry habitat, where organic carbon resources are scarce, up to two trophic levels exist. These results build off of Chapter 2, and show that *E. antarcticus* can occupy either a predator trophic position when resources are high (wet soil) or a primary consumer position when resources are low (dry soil). Since climate-driven increases in hydrological connectivity are expected to alter soil moisture and resources, the distribution and abundance of soil biodiversity and their biotic interactions in formerly dry soil habitats may ultimately shift.

In Chapter 5, I asked if the lessons learned about soil food webs in the McMurdo Dry Valleys apply to a more complex ecosystem? In this study, I used soil nematode communities from the Loch Vale Watershed (Rocky Mountain National Park, Colorado) to test whether long-term nitrogen addition affected soil food web structure and function. Results from this study indicated that a faster-cycling, bacterial food web was prevalent in N-addition plots, as evidenced by abundance of *r*-selected bacterivore nematodes. Previously, lower bacterial abundance and soil carbon were found in the N-addition plots (compared to control) and the results presented in this dissertation suggest that these changes are likely trophic. Along with Chapter 3, the evidence that I present here support the hypothesis for top-down effects of microbivore nematodes on bacteria, which is consistent in subalpine and Antarctic soils.

In summary, through both field and laboratory experiments, my PhD project has: 1) defined the soil food web structure of the McMurdo Dry Valleys using stable isotopes; 2) revealed how top down interactions affect bacteria populations and how elevated stress (e.g. soil salinity) relieves the top down pressure; 3) showed how the soil food web structure varies across the landscape of the McMurdo Dry Valleys, Antarctica as related to soil C sources; and 4) shown how nitrogen addition affects soil food web dynamics in Colorado sub-alpine soil nematode community (Loch Vale Watershed, LVWS, Rocky Mountain National Park). These results have informed our understanding of soil communities and their trophic relationships in polar and subalpine ecosystems.

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CHAPTER 1 – INTRODUCTION

Life in soil is immensely abundant and diverse. Estimates suggest that over ¼ of all living species on earth live in soil or litter (Decaëns et al. 2006). Not only is the number of organisms great, soil biodiversity is also vast. This biodiversity is often several orders of magnitude greater than that present aboveground or in the canopy of rainforests (Heywood 1995, Decaëns et al. 2006). Even a single gram of soil is estimated to contain more than 1000 taxa (Orgiazzi et al. 2016, Fierer 2017). But, much of this soil biodiversity is still undescribed (De Deyn and Van der Putten 2005) and its spatial distribution is not well understood (Phillips et al. 2017, Cameron et al. 2018). This is not limited to bacteria alone (McDonald et al. 2011); it also includes eukaryotes (Bik et al. 2012) such as fungi, protists, tardigrades, rotifers, nematodes, and arthropods.

The high biodiversity in soils makes unraveling their ecology difficult (Brussaard 1998). Their food webs are highly complex with trophic levels that range from detritivores to plant parasites to predators. Current schematics of soil food web structure often greatly simplify their trophic connections, leaving out many groups, and not accounting for species diversity (Holtkamp et al. 2008), although some recent efforts have been made to improve on this for forest soils (Digel et al. 2014). Furthermore, soil food webs contribute to ecosystem processes, but their role relative to environmental factors in controlling ecosystem functions varies spatially with shifting environmental gradients (de Vries et al. 2013). Yet, quantifying how soil biodiversity contribute to ecosystem functions remains difficult because these are often assessed at different scales depending on the process of interest (Kardol et al. 2016), which lack standardized methods (Greiner et al. 2017), and leave out groups of soil biodiversity, particularly soil fauna (García‐Palacios et al. 2014).

Due to their simplicity, Antarctic soils have been proposed as a model system in which to study soil processes and species relationships in soil food webs (Freckman and Virginia 1997, Wall and Virginia 1999). Antarctic soils contain relatively simple soil food webs compared to the highly diverse soil food webs of temperate systems (Wall and Virginia 1999). Firstly, the soil ecosystems in the McMurdo Dry Valleys, Antarctica lack complication by vascular plants, and secondly, soil fauna biodiversity is <5% that of temperate soils (Freckman and Virginia 1997). While these soil food webs are composed of soil cyanobacteria, microbes, nematodes, rotifers, tardigrades, collembolans, and mites, their distributions are heterogeneous and >90% of soils studied contain only one or two invertebrate species (Freckman and Virginia 1997, Adams et al. 2014).

Two typical soil foodwebs exist in the McMurdo Dry Valleys, Antarctica. These are: wet and dry. The "wet" soil foodwebs are associated with moss and algae mats in stream or lake margins (<5% of landscape) and have relatively high faunal diversity, which can include several genera of nematodes, tardigrades, rotifers, and microarthropods. The "dry" foodweb (~95% of landscape) has low faunal diversity (often just one nematode species, *Scottnema lindsayae*). *S. lindsayae*, a microbivore, sometimes co-occurs with other taxa, most often the nematode *Eudorylaimus antarcticus* (Freckman and Virginia 1997). Despite recognized differences in the wet and dry soil ecosystems and their food webs (Treonis et al. 1999, Ayres et al. 2007), understanding of the trophic levels and food web structure in these soils is limited. Food web structure has been illustrated (Fig 1.1, Wall and Virginia 1999); however, the specific trophic levels have not been explicitly tested and often rely on laboratory culturing studies (e.g. Overhoff et al. 1993, Adhikari et al. 2010) or mouthparts (e.g. Yeates et al. 1993) to identify feeding ecology. Furthermore, groups such as *E. antarcticus* have been identified in multiple trophic

groups (e.g. omnivorous and algivorous, Wall and Virginia 1999, Wall 2007). Resolving the trophic levels of the McMurdo Dry Valley food web structure would be a first step and would allow more general ecological questions about how biological interactions structure soil communities, and how these communities and their interactions are affected by changing environmental factors.

The aim of my PhD work has been to answer the following questions:

1) What trophic interactions are present in the McMurdo Dry Valley Soil?
2) How do environmental variables affect dry valley soil taxa and their trophic interactions?
3) How does the soil food web and its organic carbon sources vary across the McMurdo Dry Valley landscape with distance from coast and elevation?
4) Do the lessons about soil food webs learned in the McMurdo Dry Valleys apply to more complex ecosystems?

Antarctic Dry Valleys represent one of the most extreme soil habitats on earth. There are no other soil systems known where nematodes represent the top of the food chain and where food webs have so little functional redundancy (Virginia and Wall 1999). Even the nematode species richness in the Dry Valleys appears to be the lowest of any ecosystem (Freckman and Virginia 1998). Yet, lessons learned about these low-diversity soil communities can lead to insights that apply to more complex ecosystems (Wall and Virginia 1999, Wall 2007) where the functional grouping of soil invertebrates, food web modeling, and food web indices are ways to measure and simplify the vast biodiversity of soil food webs.

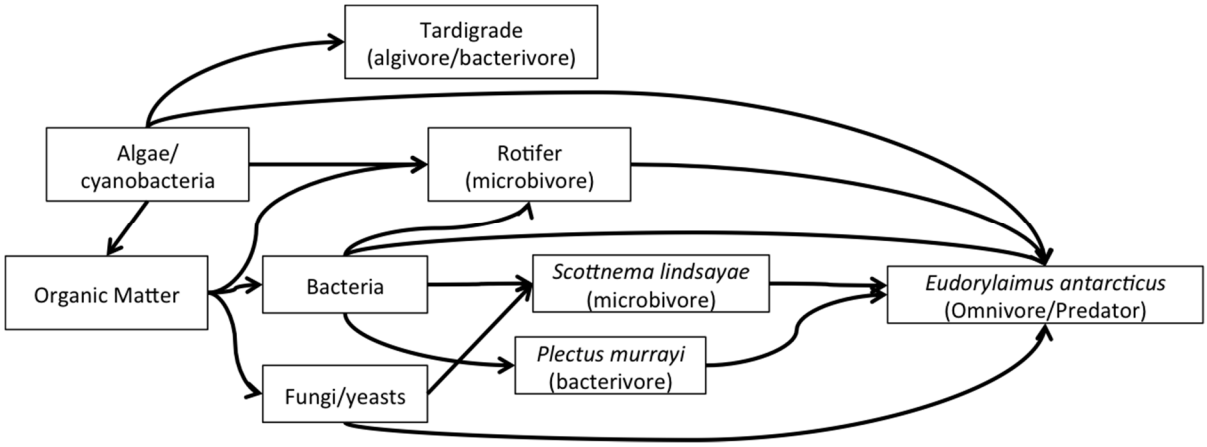

Figure 1.1 – Current illustrated understanding of the McMurdo Dry Valleys soil food web (adapted from Wall and Virginia 1999)

CHAPTER 2 – STABLE C AND N ISOTOPE RATIOS REVEAL SOIL FOOD WEB STRUCTURE AND IDENTIFY THE NEMATODE EUDORYLAIMUS ANTARCTICUS AS AN OMNIVORE-PREDATOR IN TAYLOR VALLEY, ANTARCTICA[1]

Summary

Soil food webs of the McMurdo Dry Valleys, Antarctica are simple. These include primary trophic levels of mosses, algae, cyanobacteria, bacteria, archaea, and fungi, and their protozoan and metazoan consumers (including relatively few species of nematodes, tardigrades, rotifers, and microarthropods). These biota are patchily distributed across the landscape, with greatest faunal biodiversity associated with wet soil. Understanding trophic structure is critical to studies of biotic interactions and distribution; yet, McMurdo Dry Valley soil food web structure has been inferred from limited laboratory culturing and microscopic observations. To address this, we measured stable isotope natural abundance ratios of C ($^{13}C/^{12}C$) and N ($^{15}N/^{14}N$) for different metazoan taxa (using whole body biomass) to determine soil food web structure in Taylor Valley, Antarctica. Nitrogen isotopes were most useful in differentiating trophic levels because they fractionated predictably at higher trophic levels. Using $^{15}N/^{14}N$, we found that three trophic levels were present in wet soil habitats. While cyanobacterial mats were the primary trophic level, the nematode *Plectus murrayi,* tardigrade *Acutuncus antarcticus,* and rotifers composed a secondary trophic level of grazers. *Eudorylaimus antarcticus* had a $^{15}N/^{14}N$ ratio that was 2 to 4 ‰ higher than grazers, indicating that this species is the sole member of a tertiary trophic level. Understanding the trophic positions of soil fauna is critical to predictions of current and future species interactions and their distributions for the McMurdo Dry Valleys, Antarctica.

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Introduction

The McMurdo Dry Valleys, Antarctica are an extreme ecosystem: they are very cold, dry, and windy, their soils have high pH, low moisture, low organic carbon, and are often saline (Campbell et al. 1998, Fountain et al. 1999, Burkins et al. 2001). These are simple ecosystems compared to temperate systems: they lack vascular plants, soil fauna biodiversity is 1.1 to 2.6% of temperate soils, and approximately 30-40 % of studied soils lack soil fauna (Freckman and Virginia 1997). While the presence of soil cyanobacteria, microbes, nematodes, rotifers, tardigrades, collembolans, and mites has been recorded in locations throughout the dry valleys, their distributions are patchy, with greatest invertebrate diversity in wetted lake and stream margins (Freckman and Virginia 1997, Adams et al. 2014). For example, soil invertebrates found in Taylor Valley include four species of nematode: *Scottnema lindsayae*, *Plectus murrayi*, *Geomonhystera antarcticola*, and *Eudorylaimus antarcticus*, a tardigrade, *Acutuncus antarcticus*, and rotifers. Of these, *S. lindsayae* is the only taxon whose most suitable habitat is the dry soil (Freckman and Virginia 1997, Treonis et al. 1999, Adams et al. 2006, Ayres et al. 2007) that makes up >95% of the landscape. The low biodiversity in both wet and dry soils makes each trophic link significant, due to the lower redundancy in function compared to more temperate soils (Freckman and Virginia 1997). However, *in situ* observation of feeding is difficult due to the opaque nature of soil and the small size of these fauna. The current understanding of dry valley soil trophic structure is limited to laboratory studies and microscopic observations.

Some Taylor Valley soil fauna have been grown in the laboratory, helping to identify their feeding ecology. For example, *P. murrayi* feeds on bacteria in laboratory cultures (Adhikari et al. 2010, de Tomasel et al. 2013), while the tardigrade *A. antarcticus* feeds on algae (Cecilia Milano de Tomasel, personal communication). Additionally, *S. lindsayae* is a known

microbivore, feeding on yeast and bacteria in a laboratory study (Overhoff et al. 1993). Furthermore, mouthparts are often used to identify nematode trophic groups under microscopic observation (Yeates et al. 1993). While *P. murrayi*, *S. lindsayae, G. antarcticola* all possess the tube-like esophagus of typical bacterivore nematodes, *E. antarcticus* bears an odontostylet – a piercing structure inside its mouth which can puncture food, such as plant or animal tissue. Previous studies predicted *E. antarcticus* was a likely omnivore-predator in the dry valleys (Wall and Virginia 1999) due to its mouthparts and the trophic classification of the genus *Eudorylaimus* as an omnivore-predator in temperate habitats (Yeates et al. 1993). Other Antarctic studies hypothesized that soil algae was the only food source for *E. antarcticus* (Powers et al. 1998). More recently, *E. antarcticus* was revealed to be an algal feeder through observation of chlorophyll in the intestine using a fluorescent microscope and acridine orange filter (Wall 2007). While other locations in Antarctica have predaceous taxa (Sohlenius and Boström 2005), no studies to date have confirmed a metazoan predator in Taylor Valley.

The nematode genus *Eudorylaimus* is widespread in soils (McSorley 2012). This odontostylet bearing group is considered omnivorous or predaceous in temperate ecosystems (Yeates et al. 1993, McSorley 2012, Stirling 2014). As early as 1929, Cobb observed *Eudorylaimus* feeding on mite eggs. Additionally, *Eudorylaimus* in laboratory culture preys on nematodes, such as the bacterivore genera *Acrobeloides, Plectus,* and *Panagrellus* (Tjepkema et al. 1971, Ferris and Ferris 1989), but its food sources are diverse: it also feeds on algae, enchytraeids, fungi, protozoa, and mites, but with reproduction only observed on nematodes, algae, moss, and protozoa (Hollis 1957, Wood 1973, Ferris and Ferris 1989). Its diverse feeding strategy and occupation of a top trophic position may make it an important driver of food web

structure in temperate climates. However the high taxonomic and functional biodiversity in soil makes these relationships difficult to discern.

The natural abundance of stable isotopes fractionate predictably up trophic levels at approximately +3 to 4 ‰ for $\delta^{15}N$ and +0.5 to 1 ‰ for $\delta^{13}C$ (Post 2002b, McCutchan et al. 2003). Previous stable isotope studies showed that nematode orders and families differ in their trophic structure (Kudrin et al. 2015). *Eudorylaimus antarcticus* belongs to order Dorylaimida, and Kudrin et al. (2015) found this order to have a similar isotopic composition to predaceous nematodes in boreal forests. However, in hot desert soils, Dorylaimida have isotopic composition similar to bacterivore nematodes, probably due to feeding on cyanobacteria (Darby and Neher 2012). Following this logic, we used natural abundance of stable isotopes to characterize the trophic levels for the three most abundant nematode species in Taylor Valley (*E. antarcticus*, *P. murrayi*, and *S. lindsayae*), the tardigrade *A. antarcticus*, and rotifers (grouped at phylum level). We did not include *G. antarcticola* in this study because it is an extremely rare species, and we did not find it at our study sites. We hypothesized that the grazers *P. murrayi, S. lindsayae*, *A. antarcticus*, and rotifers would be 3 to 4 ‰ for $\delta^{15}N$ and around +0.5 to 1 ‰ for $\delta^{13}C$ higher than the microbial mat values. We also expected *E. antarcticus* would be 3 to 4 ‰ for $\delta^{15}N$ and around +0.5 to 1 ‰ for $\delta^{13}C$ higher than *P. murrayi, S. lindsayae*, *A. antarcticus*, and rotifers.

Methods

To test our hypothesis, we chose a well-studied site in Taylor Valley (e.g. Spaulding and McKnight 1998, Treonis and Wall 2005) near Von Guerard stream in the Lake Fryxell basin of Taylor Valley (77.608 S, 163.254 E). In January 2014, six soil samples were collected near Von Guerard stream (Fig. 2.1). Three random soil samples (sites 1, 2, 3) were collected in dry soil

more than 5 m from the stream (but not more than 10 m) and three random soil samples (sites 4, 5, 6) were collected within 5 m of the stream (within wetted margin, but not within stream sediments). Sites 1-3 were considered 'dry' soil replicates and sites 4-6 were considered 'wet' soil replicates. These samples were collected into Whirl-Pak® bags to 10 cm using a clean plastic scoop. Approximately 500 g of soil was collected per sample. The soils were stored in an ice chest, and transported to the Crary Laboratory at McMurdo Station (United States Antarctic Program) where they were slowly cooled from +4°C to -20°C over 4 days (i.e., 24h at +4°C, 24h at -4°C, 24h at -10°C, and 24h at -20°C). Samples were shipped frozen (-20°C) to Colorado State University, Fort Collins, Colorado, USA, and slowly defrosted (as described by de Tomasel et al. 2013) before extracting soil fauna.

For each of the six sites, fauna were extracted from 100 g of soil via cold sugar centrifugation technique (Freckman and Virginia 1993). Within 48 h of extraction, taxonomic groups were identified (nematodes and tardigrades identified to species and rotifers to phylum, Olympus CKX41, 200X magnification) and counted. An additional 50-g subsample of soil was used to determine gravimetric soil moisture (water mass per unit soil mass) by mass loss from soils dried at 105°C for 48 h. The soil fauna counts were then corrected for soil moisture content and expressed kg^{-1} dry soil. After identification and enumeration, each group was separated and collected into tin capsules (8x5mm, Elemental Microanalysis BN/170056) with an eyelash tool (Superfine eyelash with handle, Ted Pella, Inc., Prod no. 113) under a dissecting microscope (Olympus SZX10, 30X magnification) per the method described by Shaw et al. (2016). A minimum of 0.02 mg biomass dry weight (approximately 50 to 100 live individuals) was collected for each taxon. For each taxon identified at each site, we aimed to triplicate fauna collections for isotope analysis. Extractions from 100 g of soil were repeated by site until

sufficient biomass was achieved for each group found at that site. For this study, it was possible to collect 8 total replicates for *E.* antarcticus (three replicates from sites 4, 5, and two replicates from site 6), 9 total replicates for *P. murrayi* (three replicates from each site 4, 5, and 6), 5 total replicates for *S. lindsayae* (two replicates from site 2, and three replicates from site 3), 9 total replicates for *A. antarcticus* (three replicates from each site 4, 5, and 6), 3 replicates for rotifers (one replicate from each site 4, 5, and 6), and 9 total replicates for the cyanobacterial mat (three replicates from each site 4, 5, and 6). Samples were dried for 48 h in a dessicator prior to shipment to the Stable Isotope Mass Spectrometry Laboratory (SIMSL) at Kansas State University for isotope analysis (CE-1110 EA coupled via Conflo II interface to an IRMS, ThermoFinnigan Delta Plus).

We also extracted *P. murrayi* from cultures grown on Bold's Modified Basal Freshwater Nutrient Media with Ottawa Sand (Adhikari et al. 2010) by both modified Baermann funnel technique, which uses water only (Hooper 1970), and the sugar centrifugation technique to check for any effect of sugar (which the fauna are submerged in for ~2 min) on the carbon isotope composition of the animals. We used 3 replicates for each extraction technique. Our tests revealed that there was no significant difference ($p = 0.25$, $df = 4$, unpaired t-test) between cultured *P. murrayi* extracted via Baermann funnel or sugar centrifugation, which had $\delta^{13}C$ isotopic compositions of -17.81 ± 0.76 and -19.26 ± 0.77 (Mean ± SE), respectively.

Results and Discussion

Across the six sites near Von Guerard stream, the nematodes *S. lindsayae*, *P. murrayi, E. antarcticus,* tardigrade *A. antarcticus,* and rotifers were found. However, their distributions were not equal across all sites. Wet sites had soil moistures of 17.91 ± 0.29 %; all groups were found

in these samples but *S. lindsayae* was in very low abundance compared to dry sites (e.g., sites 1-3; Table 2.1). Dry sites had gravimetric soil moistures of 0.70 ± 0.12 %; only *S. lindsayae* was found in these samples (Table 2.1). This is unsurprising; many studies have found *S. lindsayae* dominating dry habitat, while other taxa prefer wetter habitats in the dry valleys (e.g. Freckman and Virginia 1997, Treonis et al. 1999, Adams et al. 2006, Ayres et al. 2007).

The stable isotope composition of soil fauna biomass revealed a wet soil food web with three trophic levels: a basal level of cyanobacterial mat, a secondary level of rotifers, tardigrade *A. antarcticus*, nematode *P. murrayi*, and a tertiary level occupied by nematode *E. antarcticus* (Fig. 2.2). The primary trophic level had an overall isotopic composition of $\delta^{15}N$ -5.36 ± 0.96 ‰, $\delta^{13}C$ -24.99 ± 0.63 ‰. These cyanobacterial mats from the Von Guerard stream margin has a similar isotopic ratio to the organic matter measured by Lawson et al. (2004) for streams in Taylor Valley, Antarctica. While these mats are composed of multiple groups including cyanobacteria and diatoms, which have differing isotopic signatures (Lawson et al. 2004, Velásquez et al. 2017), our analysis is limited to composite mat samples.

The secondary trophic level at the wet sites was composed of rotifers, tardigrades, and the nematode *P. murrayi*. Generally, the trophic position of culturable groups, such as *P. murrayi* and *A. antarcticus* as revealed by stable isotopes corresponds to the established understanding of their feeding habits. The nematode, *P. murrayi*, was enriched in $\delta^{13}C$ relative to cyanobacterial mat (~ +1 ‰), but only about +2 ‰ for $\delta^{15}N$ relative to the cyanobacterial mats (Fig. 2.2). Other studies have shown the isotopic composition of Plectidae from boreal forests also support its trophic position as a bacterivore (Kudrin et al. 2015). The rotifers and tardigrades had similar isotopic compositions to each other, but differed slightly from *P. murrayi,* and are likely mat grazers (Fig. 2.2). Both were enriched $\delta^{13}C$ +0.3 to 0.5 ‰ and $\delta^{15}N$ +4 ‰ relative to

cyanobacterial mat. Cyanobacterial mats in the McMurdo Dry Valleys are highly species diverse with varying community compositions (Van Horn et al. 2016). Even Von Guerard stream's mat community varies along stream length (Van Horn et al. 2016). Furthermore, Lawson et al. (2004) showed that mats of varying species composition differ in their isotopic signatures in Taylor Valley. In maritime Antarctica, Velázquez et al. (2017) used stable isotopes to show that mat grazers feed from multiple sources, which varies by taxon. Also, *Plectus* from maritime Antarctica has been shown to selectively feed on specific taxa (Newsham et al. 2004). Differences in feeding ecology or food preferences may account for the difference in isotopic composition between *P. murrayi* and the other grazers.

The tertiary trophic level was occupied solely by *E. antarcticus*. This nematode had an isotopic composition of $\delta^{15}N$ 0.84 ± 0.44 ‰, $\delta^{13}C$ -22.23 ± 0.25 ‰ (Fig. 2.2). For $\delta^{15}N$ is an enrichment of +2.25 ‰ relative to rotifers and tardigrades and +4 ‰ relative to *P. murrayi*. The order Dorylaimida are usually considered omnivore-predators, but have also been shown to eat bacteria, fungi, algae and plants (Freckman 1988, Yeates et al. 1993, Kudrin et al. 2015). Protozoa may also be a possible food source for nematodes and although present in dry valley soil (Bamforth et al. 2005), were not included in this study due to difficulty in isolating individuals and collecting sufficient biomass for isotope measurement. Given our isotope results and that *E. antarcticus* also eats algae (Wall 2007), it should be described as an omnivore-predator for the McMurdo Dry Valleys.

The dry soil food web had the lone consumer *S. lindsayae*, a microbivore nematode (Overhoff et al. 1993). *Scottnema lindsayae* had an isotopic composition of $\delta^{15}N$ -4.18 ± 1.05 ‰, $\delta^{13}C$ -27.91 ± 0.39 ‰ (Fig. 2.3), which is considerably lighter than consumers in the wet food web (Fig. 2.2), making the wet soil's cyanobacterial mats an unlikely primary level for dry soil.

Other studies have suggested that lithic primary producers (e.g. cryptoendoliths, hypoliths) could be a carbon source in dry soils (Burkins et al. 2000), and these sources have a lower isotopic signature than lake and stream-associated cyanobacterial mats (Burkins et al. 2000). Additionally, we did not find *E. antarcticus* in the dry soil sites, but it is occasionally found in dry soil in the dry valleys (Freckman et al. 1997). The most frequent two-species community in the dry valleys is *S. lindsayae* with *E. antarcticus* (Freckman and Virginia 1997). Further work is needed to confirm trophic positions of soil fauna across the heterogeneous dry valleys landscape, especially in habitats with varied carbon sources (Burkins et al. 2000) and communities of multiple invertebrate species.

Our results have ecosystem implications. Around 95% of the McMurdo Dry Valleys region is considered dry soil habitat (=<2% gravimetric water content), which is most suitable for the dominant nematode, bacterivore *S. lindsayae*. While *E. antarcticus* are present in low abundance in dry soil habitat, many are found in moist or wet soils. Around 5% of the McMurdo Dry Valleys are considered moist soil habitat, which is most suitable for *E. antarcticus* (Virginia and Wall 1999, Burkins et al. 2001). The McMurdo Dry Valleys have recently been termed, "a landscape on the threshold of change" because significant increases in the loss of both glacier and buried ice are expected to occur (Fountain et al. 2014). This predicted future increase in glacial melt and permafrost thaw will produce larger amounts of liquid water during the austral summer, generally "wetting up" what is now dry landscape (Gooseff et al. 2017b).With this increased melt from glaciers, massive buried ice and permafrost, moist habitat area should increase. Such a change could impact the distribution and abundance of soil fauna, which differ in their habitat preferences (Freckman and Virginia 1997), altering community composition (Nielsen et al. 2011), and ultimately having ecosystem level impacts on soil processes including

carbon cycling (Barrett et al. 2008, Gooseff et al. 2017a). Understanding trophic positions and biotic interactions of soil fauna is critical for predicting future changes in species distributions and interactions due to increased connectivity.

Table 2.1: Abundance of taxonomic groups from Taylor Valley soil samples in total live individuals kg^{-1} dry soil. Data are shown as mean ± standard error. Dry soil (n=3) corresponds to samples 1, 2, and 3, which were >5m from the stream (soil moisture <1% gravimetric). Wet soil (n=3) corresponds to samples 4, 5, and 6, which were <5m from the stream and had soil moisture >17% (gravimetric).

Taxonomic Group	Overall Abundance	Dry Soil Abundance	Wet Soil Abundance
Nematoda			
Scottnema lindsayae	1822.98 ± 213.22	533.07 ± 402.76	54.59 ± 54.59
Plectus murrayi	300.23 ± 172.73	0.00 ± 0.00	600.45 ± 243.00
Eudorylaimus antarcticus	1325.61 ± 640.76	0.00 ± 0.00	2651.22 ± 543.74
Tardigrada			
Acutuncus antarcticus	545.67 ± 287.81	0.00 ± 0.00	1091.33 ± 341.23
Rotifera			
	1299.48 ± 667.53	0.00 ± 0.00	2598.95 ± 734.38

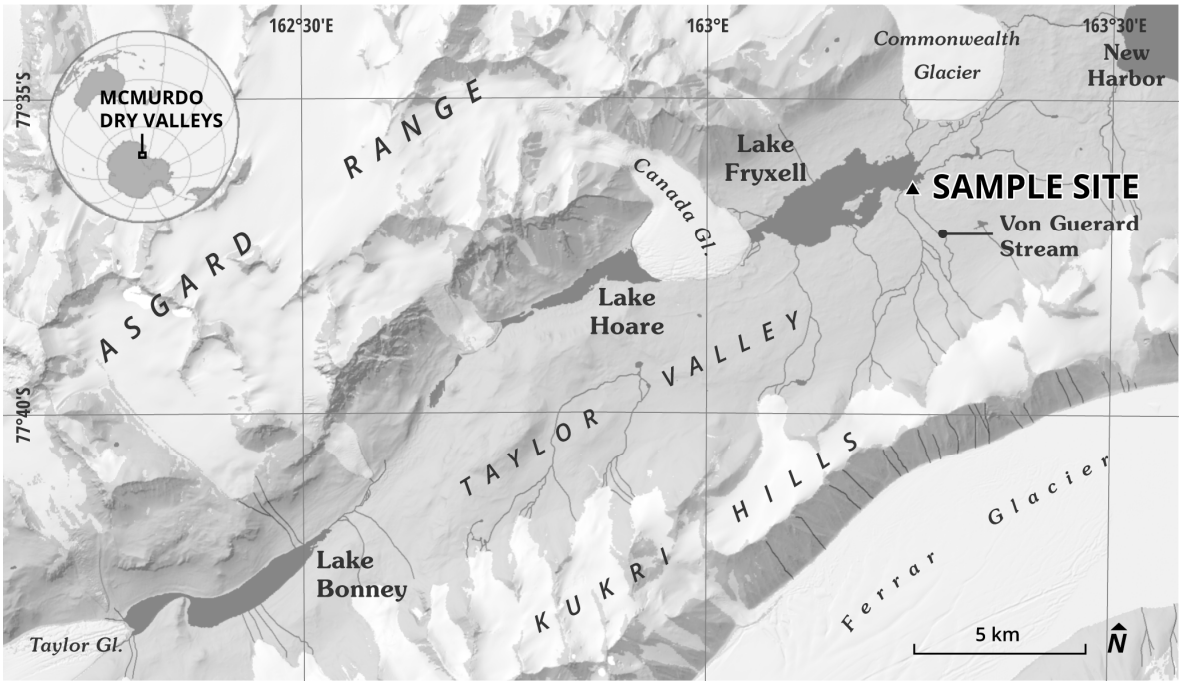


Figure 2.1: Location of our sample site near Von Guerard stream in the Lake Fryxell basin in Taylor Valley, Antarctica. Taylor Valley is located in the McMurdo Dry Valleys of Southern Victoria Land, Antarctica (inset). Map by Brad Herried, Polar Geospatial Center.

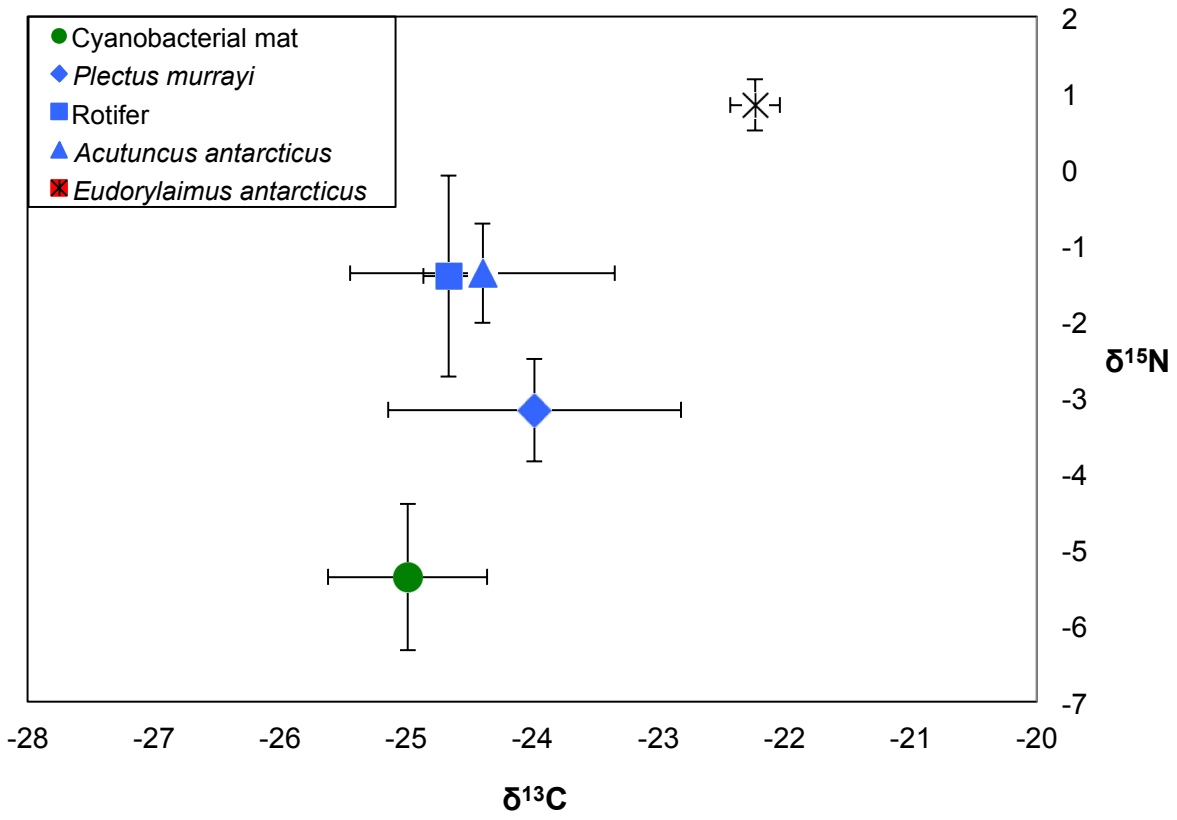


Figure 2.1: δ ^{13}C and δ ^{15}N signature of fauna groups from wet soil within 5 m of Von Guerard stream in Taylor Valley, Antarctica. Data presented are ‰ and are means with standard error bars.

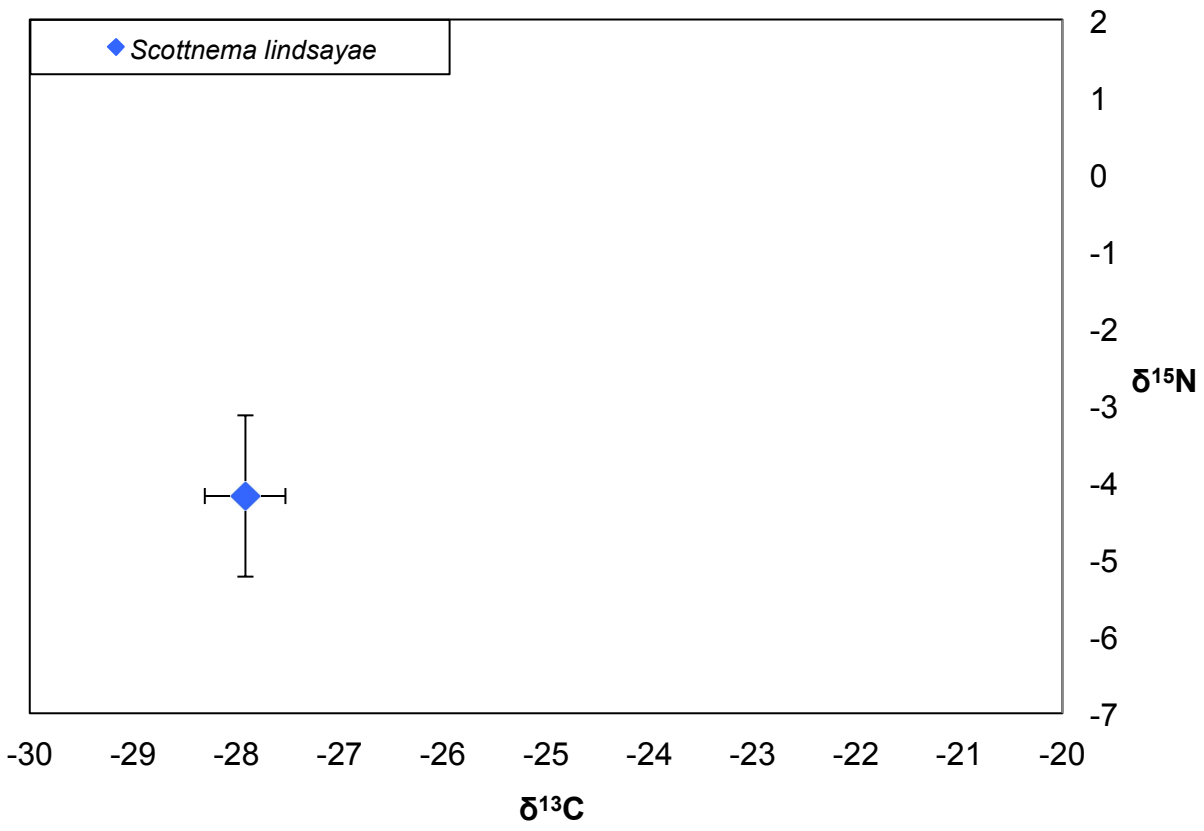


Figure 2.2: δ ^{13}C and δ ^{15}N signature of fauna groups from dry soil 5 to 10 m from Von Guerard stream in Taylor Valley, Antarctica. Data presented are ‰ and are means with standard error bars.

CHAPTER 3 – BIOTIC INTERACTIONS IN EXPERIMENTAL ANTARCTIC SOIL MICROCOSMS VARY WITH ABIOTIC STRESS

Summary

Biotic interactions structure ecological communities worldwide and abiotic stress affects the strength of these relationships. These interactions are difficult to study in soils due to the shear amount of biodiversity and the myriad factors that affect soil species, including aboveground life. Thus, there is little research on how the strength of trophic interactions in soils varies with environmental conditions. The McMurdo Dry Valleys, Antarctica are relatively simple soil ecosystems compared to temperate soils, making them an excellent study system for addressing questions on soil's trophic relationships. Soil microbes and relatively few species of nematodes, rotifers, tardigrades, springtails, and mites are patchily distributed across the landscape, which is devoid of vascular plants and vertebrates. The trophic structure of these soil food webs span from microbes to microbivore and omnivore-predator invertebrates. However, to date, whether these biotic interactions have a role in community structure or if their trophic relationships change with abiotic stress is still unknown. The McMurdo Dry Valley Long Term Ecological Research program data show that *Scottnema lindsayae,* a microbivore nematode*,* and *Eudorylaimus antarcticus*, an omnivore-predator nematode, are negatively associated with increased soil salinity, but have opposite responses to increased soil moisture (negative and positive, respectively). However, the magnitude of their responses differs. To test how increased moisture and salinity affect soil invertebrates and subsequently influence their biotic interactions in this cold desert, we established a laboratory microcosm experiment in a full factorial design (4 community x 2 moisture x 2 salinity treatments). Community treatments were 1) Control (bacteria only), 2) *Scottnema (S. lindsaye* + bacteria*)*, 3) *Eudorylaimus* (*E. antarcticus* +

bacteria), and 4) Both (*S. lindsayae* with *E. antarcticus* + bacteria). Salinity and moisture treatments were control and high. *Eudorylaimus antarcticus* did not survive microcosm establishment except in the Both community treatment. Elevated moisture significantly reduced the abundance of adult *S. lindsayae*, but not the total population of *S. lindsayae*. Elevated salinity significantly reduced the total population of *S. lindsayae*, including juveniles and females, but not males. We found that *S. lindsayae*, exerted top-down control over soil bacteria populations, but this effect was dependent on the salinity treatment. In the high salinity treatment, soil bacteria were released from top-down pressure. Ours is the first study to confirm, although in lab microcosm conditions, top-down control in the MDV soil food web.

Introduction

How biological interactions affect communities is a key research theme in ecology. Biotic interactions are ubiquitous in most terrestrial ecosystems, and interact with abiotic factors and dispersal to determine populations and community structure (Maestre et al. 2010). For example, studies have shown how biotic interactions affect plants (Maestre et al. 2010), benthic invertebrates (Kolar and Rahel 1993), and bird communities (Heikkinen Risto et al. 2007) under varying environmental conditions, but relatively few studies have empirically examined how biotic interactions affect soil community structure and function (but see Coleman et al. 1977, Wall and Moore 1999). This is partly due to the vast biodiversity in soils, whose relationships are further confounded by many interacting factors including plants and aboveground animals.

The McMurdo Dry Valleys (MDV) in Victoria Land, Antarctica compose the largest ice-free area on the continent (Fountain et al. 1999). Among the world's harshest environments, they are a simple ecosystem with very limited diversity of eukaryotes (Freckman and Virginia 1997,

Treonis et al. 1999) compared to temperate ecosystems, making them an excellent system in which to study soil communities (Wall 2007). There are no vascular plants or vertebrates, and the metazoan diversity includes just a few species of nematodes, rotifers, tardigrades, collembolans, and mites (Adams et al. 2006, Adams et al. 2014), the most abundant of which is a nematode (Freckman and Virginia 1997, Wall and Virginia 1999). Low temperatures, low water, low organic carbon availability, and high salinity are factors known to constrain life in the MDV (Wall and Virginia 1999, Courtright et al. 2001, Poage et al. 2008). However, these factors are shifting across the landscape due to climate-induced changes (Fountain et al. 2014). For example, elevated solar radiation and episodic warming has altered the availability of liquid water through melted buried ice, higher stream flows, expanded stream margins, and the formation of shallow groundwater transports, e.g. water tracks (Fountain et al. 2016). When water reaches previously dry soils, it liberates and mobilizes soil nutrients and salts, weathers soil, and stimulates primary productivity in newly wetted areas, significantly altering soil properties that affect soil biota (Ball et al. 2011, Ball and Virginia 2012, Ball and Levy 2015). Greater hydrological connectivity through the formation of more abundant streams and water tracks is predicted for the future (Gooseff et al. 2017b), and could alter soil habitats and their biodiversity landscape-wide.

Previous work has shown that abiotic factors explain a large part of the variation in invertebrate populations and community structure in the MDV. Along with other factors such as pH and carbon availability, moisture and salinity affect microbes and invertebrates from population to ecosystem (see Table 3.1; Courtright et al. 2001, Barrett et al. 2006, Poage et al. 2008). Dry habitat (~2-3% gravimetric water content) is dominated by an endemic, microbivore nematode, *Scottnema lindsayae*. This nematode co-occurs with other invertebrates such as the

omnivore-predator nematode *Eudorylaimus antarcticus*, and sometimes with the nematode *Plectus murrayi* along with tardigrades and rotifers. However, *P. murrayi*, *E. antarcticus*, tardigrades, and rotifers prefer wet habitat and *S. lindsayae* is most frequently found in single species communities in dry soils (Treonis et al. 1999, Courtright et al. 2001). When soil moisture increases in dry soil, *E. antarcticus* and *P. murrayi* populations often increase while *S. lindayae* populations decrease (Freckman and Virginia 1997), but the long-term ecosystem response differs when wetting occurs as an extreme pulse event (Nielsen et al. 2012, Andriuzzi et al. 2018) or as a long-term press (Gooseff et al. 2017a). Andriuzzi et al (2018) showed that long-term climate-associated increases in soil moisture have detrimental effects on the dominant nematode, *S. lindsayae*, and marginal positive effects on the other taxa.

Salinity co-varies with soil moisture and these two factors interact to affect invertebrates. For example, moisture facilitates the movement of solutes and thus alters the salinity of habitats. In drier soils, elevated soil salinity reduces water availability and puts osmotic pressure on MDV biota (Andriuzzi et al. 2018). In newly wetted areas, the magnitude of changes to soil moisture and salinity and their interaction can result in either an increase or a decrease in biological activity (Wynn-Williams 2000). Soil salinity is a primary driver of nematode populations in the MDV and affects taxa differently (Ball and Virginia 2012). This may be because of physiological stress and especially nitrogen toxicity on nematodes (Courtright et al. 2001, Nkem et al. 2006, Poage et al. 2008). Poage et al (2008) found that *S. lindsayae* were more abundant in saline soils than the nematodes *E. antarcticus* or *P. murrayi,* but that mortality of all species increases as salinity increases. However, *Scottnema lindsayae* is more tolerant of increased salinity than other species (Nkem et al. 2006). Besides mortality, the effect of high salinity on soil water potential may cause nematodes to become inactive and decoupled from

ecological processes (Treonis and Wall 2005). Nematodes are able enter a state of suspended animation called anhydrobiosis as a desiccation survival strategy (Crowe and Madin 1975, Freckman and Womersley 1983). Treonis and Wall (2005) showed that the proportion of the nematode community in anhydrobiosis was positively correlated with increasing soil salinity in the dry valleys. In addition to physiological stress on nematodes, soil salinity and moisture likely also have trophic effects on nematodes through their food availability. For example, soil salinity is an important driver of microbial communities in the MDV (Nkem et al. 2006) and other ecosystems (Van Horn et al. 2014), where salinity can be toxic to microbial metabolism through extracellular enzyme denaturation or changes to cell ion balance (Lozupone and Knight 2007, Wang et al. 2011).

The effects of salinity and moisture on soil invertebrates are likely twofold: 1) physiological and 2) trophic. Previous research provides evidence for direct physiological effects of water and salt on soil invertebrates and microbes (Table 3.1), but it is also plausible that any effect on microbes could indirectly affect their invertebrate consumers and vice versa. While evidence for biotic interactions' roles in community structure and/or ecosystem functions have not been documented in the MDV, Hogg et al (2006) suggested that patterns of invertebrate co-occurrence could be coincidental due to the shared basic requirement for suitable soil moisture. Recent evidence shows that *E. antarcticus* occupies the omnivore-predator trophic level in Taylor Valley (Shaw et al. 2018). The presence of multiple trophic levels – from microbes, to microbivores, to omnivore-predators – suggests that biotic interactions are present in the MDV. Whether or not these biotic interactions are significant drivers of community structure or how these interactions change under varying environmental conditions is still undetermined.

We asked: 1) How does soil moisture and salinity affect populations of bacteria, *S. lindsayae*, and *E. antarcticus*? 2) Does the strength of their biotic interactions shift with abiotic stress? To test these questions we designed a fully crossed laboratory microcosm experiment (4 community x 2 moisture x 2 salinity treatments) to test the effects of soil salinity, moisture, and their interaction on bacteria, *S. lindsayae*, and *E. antarcticus* at four levels of community diversity (bacteria only, bacteria+*S. lindsayae* only, bacteria+*E. antarcticus* only, and bacteria + both nematode species). We hypothesized that 1) elevated moisture would have a positive effect on soil bacteria, a positive effect on *E. antarcticus*, but a negative effect on *S. lindsayae*, 2) elevated salinity would negatively impact all biota, and 3) the magnitude of responses would vary by community. Specifically, we expected bacterial abundance to be negatively related to the abundance of total nematodes, and the response of *S. lindsayae* to depend on the response of *E. antarcticus* in the community treatment with both nematode species.

Methods

Study site

The McMurdo Dry Valleys are a cold desert with mean annual temperature of -16 to -20°C and <10 cm mean annual precipitation annually (Clow et al. 1988, Fountain et al. 1999, Doran et al. 2002, Fountain et al. 2009). Glaciers, large areas of arid soils, polygons (patterned ground caused by freeze-thaw), permanently ice-covered lakes, and seasonal glacial meltstreams make up the MDV landscape. The McMurdo Dry Valleys Long Term Ecological Research (LTER) project has been collecting data on this ecosystem through monitoring studies and experiments since 1993. Data include biological, geochemical, and climatic variables. The MDV LTER is primarily located in Taylor Valley (77 S, 162 E), which expands ~35km from the Polar

Plateau to the Ross Sea. The soils of Taylor Valley are gelisols, generally over 95% sand with very low soil organic matter (<2 g /kg) and high salinity (Clow et al. 1988, Fountain et al. 1999, Doran et al. 2002, Fountain et al. 2009). The summer air temperature is frequently >0°C, and liquid water is present annually as soil pore water and meltstreams.

Twenty-five 500g surface soil samples (10cm depth) were collected in January 2015 near Many Glaciers Pond in Taylor Valley, Antarctica (77.598 S, 163.323 E) for microcosm set up. An additional 10 bulk soil samples were collected from moss beds at Hjorth Hill (77.539 S, 163.562 E) to provide nematodes for the community treatments. Prior to microcosm set-up, soils were shipped to and stored frozen (-20°C) at Colorado State University. At collection, these soils were 107.51 ± 1.03 uS/cm electrical conductivity (a proxy for soil salinity) and 2.94 ± 0.63 % soil moisture (gravimetric). Electrical conductivity (EC) was determined using a 5:1 water to soil dilution, mixing (10s), and reading EC (uS/cm) using a conductivity meter. Gravimetric soil moisture (water mass per unit soil mass) was determined via mass loss from a 10-g soil subsample dried at 105°C for 48 h.

Microcosm set-up

Using the bulk soil collected from the McMurdo Dry Valleys, community (4 levels), moisture (2 levels), and salinity treatments (2 levels) were applied in a full factorial design with 5 replicates (4 x 2 x 2 x 5 = 80). Community treatments were Control (bacteria only), *Scottnema* (bacteria + *S. lindsayae*), *Eudorylaimus* (bacteria + *E. antarcticus*), and Both (bacteria + *S. lindsayae* and *E. antarcticus*). Moisture treatments were high moisture (~8% g/g soil moisture) and control moisture (~3% g/g soil moisture). Salinity treatments were high salinity (~600 uS/cm) and control salinity (~100 uS/cm). For the soil moisture treatments, 8% gravimetric soil moisture level was chosen as the 'high moisture' treatment because it is representative soil

moisture levels in stream and lake margins, and in water tracks (Treonis et al. 1999, Ayres et al. 2007, Ball and Virginia 2012). We considered 3% soil moisture (gravimetric) as the control soil moisture because soils were 2.94 ± 0.63 % moisture at collection. Additionally, we wanted nematodes to be active in both our control and wet treatments, and activity drops off as nematodes enter anhydrobiosis at <2% moisture (Treonis and Wall 2005). We chose 600uS/cm electrical conductivity as our 'high salinity' treatment because models suggest that this level negatively affects both *S. lindsayae* and *E. antarcticus* populations, but does not cause complete mortality (Poage et al. 2008). Soil collected for the microcosms had background electrical conductivity of 107.51 ± 1.03 uS/cm, and we considered this the control salinity.

The 25 bulk soil samples from Many Glaciers Pond were homogenized and used for microcosm set-up in March 2017 (2kg soil was reserved for nematode extraction). A total of 10kg of bulk soil was combined in large aluminum trays and defaunated by heating soil at 65°C for 48h (Franco et al. 2017). Next, 125g of soil were added to 80 pre-autoclaved glass mason jars (1Pint size). After soil was added, microcosms were chilled for 24h (4°C). Then all microcosms were inoculated with bacteria using a soil slurry method (Setälä and Huhta 1991, Bouwman et al. 1994, Laakso et al. 2000). Briefly, 150g of fresh soil was mixed with 800mL of cold (4°C) sterile deionized water in a pre-sterilized 1000mL beaker on a stir plate for 45min. This water was passed though a 25-micron (500 mesh) sieve to remove any nematodes, but allow bacteria to pass through. Next, 7mL of microbial inoculant was added to each jar with a sterile pipette. Microcosms were placed into a 4°C incubator for 2 weeks to allow bacteria to establish before moisture, salinity, and community treatments were added.

For the community treatments, *S. lindsayae* was extracted from twenty replicates of 100g soil from the bulk soil collected at Many Glaciers Pond via cold sugar centrifugation method

(Freckman and Virginia 1993) and counted under an inverted microscope (Olympus CKX41). Approximately 8500 total *S. lindsayae* were available for inoculation of 40 microcosms. Next, these nematodes were pooled in a falcon tube, allowed to settle for an hour, and then the total volume was reduced to 20mL with an aspirator. The supernatant was reserved in a separate falcon tube and examined under the microscope to ensure no nematodes were present. Using the vortex on the lowest setting, nematodes were gently mixed and 0.5mL of water + nematodes was pipetted into to each *Scottnema* and Both treatment microcosm. During inoculation, five samples were counted at random, where the 0.5mL inoculant was pipetted directly onto a counting dish. An average of 180 ± 10.5 live *S. lindsayae* were present in the inoculant per microcosm. Then, 0.5mL of the reserved nematode-free supernatant was added to the remaining microcosms (*Eudorylaimus* and Control treatments) to account for the effect of any bacteria or nutrients present in the water.

Because very few *E. antarcticus* were present in the Many Glacier Pond soil, ten bulk soil samples collected from moss beds in 2015 at Hjorth Hill were used for extraction and collection of *E. antarcticus* for the *Eudorylaimus* treatment. Ten replicates of 100g of soil were extracted and counted under the inverted microscope. Many *E. antarcticus* were present, along with *Plectus murrayi*, rotifers, and tardigrades. Due to the biodiversity in these samples, *E. antarcticus* were picked by hand using an eyelash tool (Superfine eyelash with handle, Ted Pella, Inc., Prod no. 113). Approximately 2100 live *E. antarcticus* were hand picked into a single falcon tube with water. Then *Eudorylaimus* and Both treatments were established the same way as *Scottnema* treatment (described above). Five test samples were counted during inoculation, and each contained an average of 52 ± 4.3 live *Eudorylaimus*. Again, 0.5mL of the reserved

supernatant containing no nematodes was added to the remaining microcosms (*Scottnema* and Control community treatments).

After community treatments were applied to microcosms, salinity and moisture treatments were added. We added 50mg NaCl to the High Salinity treatments to bring the soil electrical conductivity from ~100uS/cm up to ~600 uS/cm. Microcosms that did not receive NaCl (e.g., Control) were removed from the incubator for the same amount of time to account for any effects of movement or brief temperature changes. We added 2mL of sterile, deionized water to the High moisture treatments to bring gravimetric soil moisture up to ~8% (g water/g dry soil). Dry treatments were weighed and placed in a dessicator (inside the incubator) until moisture levels were ~3% (g water/g dry soil). Microcosms were weighed every 2 weeks to check moisture levels and sterile deionized water was added as needed.

Microcosms were incubated at 8°C for three months, approximately the length of one active season (Fountain et al. 1999).. Then, microcosms were destructively harvested. Soil subsamples were taken in the following quantities for analyses: 5g for bacteria extraction, 100g for nematode extraction, 10g for soil moisture, and 10g for electrical conductivity. All extra soil was placed in sterile whirlpac bags and frozen (-20°C). Direct counts of bacteria cells were assessed via epi-fluorescent microscopy (as in: Bloem 1995, Frey et al. 1999, Sistla et al. 2013). Nematodes were extracted via sugar centrifugation method (Freckman and Virginia 1993) and then nematode abundance was assessed via bright-field microscopy (Olympus CKX41). Nematodes were identified to species, sex, and life stage (e.g., adult or juvenile).

Data analysis

Nematode counts were standardized to soil mass and expressed as the number of individuals kg dry soil^{-1}. Bacterial cells were calculated to number of cells g dry soil^{-1}. A three-

way ANOVA was used to test the effects of moisture, salinity, and community treatments on nematode and bacteria populations. Specifically, bacterial abundance, *S. lindsayae* total abundance, *E. antarcticus* total abundance, and *S. lindsayae* juveniles, *S. lindsayae* adults, *S. lindsayae* females, and *S. lindsayae* males were assessed with F tests followed by post hoc tests (Tukey HSD) to confirm significant effects ($p < 0.05$). Residuals were tested for normality of distributions via Q-Q plots and Shapiro-Wilks tests, and data were log (x+1) or square root transformed if they failed (rejected when Shapiro-Wilks $p<0.05$). Specifically, square-root transformation was chosen for bacterial cells, and log (x+1) was chosen for *Eudorylaimus* abundance. *Scottnema* abundances met assumptions of normality and were not transformed. The relationships between a) nematode and bacteria abundance and b) *S. lindsayae* abundance and *E. antarcticus* abundance were tested via linear models. All analyses were done using R 3.1.3 (R Core Development Team 2013).

Results

Microcosm establishment

An average of 180 ± 10.5 *S. lindsayae* were added to *Scottnema* and Both community treatments, but overall, 71 ± 4.1 survived to the end of the experiment. An average of 52 ± 4.3 *E. antarcticus* were added to *Eudorylaimus* and Both community treatments, but very few survived (<1%). At the end of the experiment, gravimetric soil moisture (% g/g) was 3.93 ± 0.17 (mean ± S.E.) for the dry soil treatment and 6.48 ± 0.25 (mean ± S.E.) for the wet treatment. Electrical conductivity of the control soil was 107.51 ± 1.03 uS/cm while electrical conductivity of the High Salinity treatment was 612.33 ± 4.94 uS/cm.

Effect of treatments on nematodes and bacteria

There were significant overall effects of the community treatments and a significant interaction between community and salt treatment on total bacteria (Table 3.2). Moisture treatment did not significantly affect bacterial abundance (LSMeans, p=0.827). There were significantly less bacterial cells in the Control, *Scottnema,* and Both community treatments compared to the *Eudorylaimus* treatment in Control salinity microcosms (LSMeans, $p<0.05$), but this effect was diminished under the high salt treatment (Fig 3.1). Furthermore, there were significantly more bacterial cells present in the high salinity treatment for the *Scottnema* and Both community treatment compared to the *Scottnema* and Both community treatments with low salinity (Fig 3.1; LSMeans, $p<0.05$).

There were significant overall effects of the salinity treatment, but not moisture or community treatment on *S. lindsayae* abundance (Table 3.2). Total *S. lindsayae* abundance was significantly less in the elevated salt treatment compared to the control (LSMeans, p=0.02; Fig 3.2A). This effect was particularly evident for juveniles and females (LSMeans, p= 0.042 and 0.004, respectively; Fig 3.2A), but not for males (LSMeans, p=0.168; Fig 3.2A). While there was no significant moisture treatment effect on the total population (Table 3.2), there were significantly less adult *S. lindsayae* in the wet treatment compared to the dry treatment (LSMeans, p=0.041), but this effect differed by community and salinity treatment (Fig 3.2B). The moisture treatment did not affect the total abundance of juveniles (LSMeans, p=0.498). *Scottnema lindsayae* was added to two of the community treatments: Both and *Scottnema*. There were no differences in the total abundance of *S. lindsayae* between these two treatments (LSMeans, p=0.198).

Eudorylaimus antarcticus did not survive in most microcosms (was <1%). One single microcosm had 3 living *E. antarcticus*, this was the greatest survival of *E. antarcticus* (Both community, Control salinity, Wet). Eleven other microcosms had 1 or 2 living *E. antarcticus*, and all but two of these were the Both community treatment. Thus, the only treatment where *E. antarcticus* has significant survival was the Both community treatment (Fig 3.3), making the community treatment the only significant effect on *E. antarcticus* abundance (Table 3.2).

Bacteria declined as *S. lindsayae* density increased up to ~500 individuals kg dry soil^{-1} and then bacteria populations leveled off (Fig 3.4A, $p < 0.05$, $r^2 = 0.229$). However, this relationship depended on salinity treatment. In the control salinity treatment, the linear relationship between bacteria and *S. lindsayae* abundance was not significant (Fig 3.4B, $p = 0.402$, $r^2 = 0.050$). But in the high salinity treatment, the bacteria abundance was significantly greater as *S. lindsayae* abundance declined (Fig 3.4B, $p = 0.020$, $r^2 = 0.333$). Due to the low survival of *E. antarcticus*, a linear relationship between the abundance of *E. antarcticus* and *S. lindsayae* was not assessed (Fig 3.4C).

Discussion

Antarctica's McMurdo Dry Valleys are among the coldest and driest terrestrial ecosystems in the world, making this habitat one of the harshest to support life. Here, little evidence of biotic interactions has been found (Hogg et al. 2006) and prior research has focused primarily on the relationship between abiotic factors and soil biodiversity. Four genera of nematodes co-occur across the MDV and include microbivores and an omnivore-predator. These nematodes co-occur with other invertebrates, tardigrades and rotifers. *Scottnema lindsayae*, a microbivore, is the most common nematode in the MDV, most commonly found in dry soil

communities as the only metazoan species; however the second most common community in dry soil is *S. lindsayae* with *E. antarcticus*, the omnivore-predator (Freckman and Virginia 1997). While the presence of two to three trophic levels (microbes, microbivores, omnivore-predators) indicates that biotic interactions occur in the MDV, biotic interactions have not been identified as significant drivers of communities or ecosystem function.

Effects of salinity and moisture on populations of bacteria and nematodes

We hypothesized that elevated soil moisture would have a positive effect on soil microbes and *E. antarcticus*, and a negative effect on *S. lindsayae*, but we found that moisture had no effect on bacteria and a negative effect on *S. lindsayae* adults only. A decline in the adults is an indication that future fecundity could be negatively impacted. In other words, a decrease in adult nematodes could have lag effects through reduced reproduction, which negatively impacts future populations. Moisture has been shown to have a negative impact in field studies on dry-soil adapted *S. lindsayae* (Wall 2007), but these effects either occurred with an extreme flooding event when the soil became saturated (e.g. Nielsen et al. 2012) or over a decade, when the populations decline steadily (Andriuzzi et al. 2018). Since our microcosm study mimicked the length of one 'active' season, and *S. lindsayae* generation time likely occurs over multiple seasons (e.g. Porazinska et al. 2002, Nielsen et al. 2012, Andriuzzi et al. 2018), it likely would have taken longer to see a moisture effect on the total *S. lindsayae* population.

Our results show that the relative high soil salinity had significant negative effects on total S. *lindsayae* abundance as well as juveniles and females (Fig 3.2A), which could impact long term populations through an effect on reproduction and recruitment to adulthood (Overhoff et al. 1993). In other studies, not only nematode survival but also nematode activity was affected by soil salinity. Treonis and Wall (2005) found a significant relationship between the number of

nematodes in anhydrobiosis (a form of cryptobiosis) and soil water potential, which is affected by the interaction between soil water and salt content. Furthermore, the response of *S. lindsayae* to elevated soil salinity *in situ* is likely to depend on the type and composition of salts, which are often more toxic than NaCl alone (Nkem et al. 2006)

Scottnema lindsayae ***grazing inhibits bacterial response to dead nematodes***

Carbon availability may be a significant limitation for bacterial biomass even when other conditions are favorable (low salinity, suitable moisture). As Van Horn (2014) found, microbes quickly take advantage of a new carbon source when it becomes available, especially in areas of low salinity. In our study, bacterial abundance was significantly higher in the *Eudorylaimus* community treatment (Fig 3.1) over the other three treatments in control salinity. In this treatment, effectively all of the ~50 nematodes added died during the experiment (1 microcosm had a single survivor), and were presumably decomposed by bacteria. When no nematodes were added, and thus no new carbon was added in the Control community treatment, the bacterial abundance was lower (Fig 3.1). Bacteria were inhibited when living *S. lindsayae* were present, as there was no difference in number of cells for the Both community treatment compared to the Control, despite high *E. antarcticus* mortality, suggesting that *S. lindsayae* grazing inhibits bacterial response to the elevated carbon provided by dead *E. antarcticus*.

Biotic interactions between **Scottnema lindsayae** ***and soil bacteria depends on salinity treatment***

We hypothesized that the magnitude of responses would vary by community, driven by biotic interactions. We expected bacterial abundance to be negatively related to the abundance of total nematodes. We found that the number of bacterial cells declined with increasing abundance of total living *S. lindsayae*, but this relationship leveled off at >500 *S. lindsayae* per kg dry soil

(Fig 3.4A). Furthermore, this relationship differed depending on the salinity treatment. In the control soil alone, there was no relationship between bacteria cells and *S. lindsayae* abundance, suggesting a more stable bacteria population or a constant rate of *S. lindsayae* activity (Fig 3.4B). In the high salt treatment, bacteria abundance was significantly correlated to *S. lindsayae* abundance (Fig 3.4B), with bacteria abundance increasing as *S. lindsayae* declined, suggesting a release of top-down pressure on bacteria.

We expected the response of *S. lindsayae* to depend on the response of *E. antarcticus* in the community treatment with both nematode species. Due to the low survival of *E. antarcticus,* we were unable to evaluate our last hypothesis. The only significant survival of *E. antarcticus* occurred when *S. lindsayae* was present (Fig 3.3), but even this survival was very low. This could be due to a number of stresses including transferring the nematodes from Hjorth Hill soils to Many Glaciers Pond soil, the stress of picking the nematodes by hand with the eyelash tool, or providing insufficient food sources. Similarly, labs that culture other Antarctic nematodes have been unable to keep *E. antarcticus* alive in culture (C. Tomasel personal communication, B. Adams personal communication). Nkem et al. (2006) found a negative relationship between *S. lindsayae* and *E. antarcticus* in a field survey, and suggested that this could be due to either a biological interaction or differing habitat requirements. Testing the biotic relationship between *S. lindsayae* and *E. antarcticus* and how this relationship is affected by environmental factors will require additional studies.

Biotic interactions – including competition, predation, and facilitation – are among the primary drivers of ecological community structure in ecosystems worldwide. The relative importance of these drivers differs across various ecosystems and depends on a suite of factors that influence strength of interactions. Not only have recent climate changes altered nematode

populations and community structure (Porazinska et al. 2002), but the long-term effects of these changes are predicted to impact trophic structure and the strength of biotic interactions in the MDV (e.g. Gooseff et al. 2017a, Andriuzzi et al. 2018). Recent research suggested top-down effects of *S. lindsayae* on soil bacteria abundance (Nielsen et al. 2011), but until now, these effects have been unconfirmed. Ours is the first study to demonstrate, although in lab microcosm conditions, top-down control in the MDV soil food web through *S. lindsayae*'s effects on bacterial abundance. Furthermore, our results show that biotic interactions are significantly altered by abiotic stress, specifically salinity. This has large implications for MDV biodiversity, where a future ecosystem is expected experience a new distribution of soil solutes with changing hydrological connectivity.

Table 3.1. Effects of salinity and moisture on soil taxa from population to ecosystem.

Level	Taxa	Effects	Citations
Populations			
	Microbes	-Gene expression of AOA or AOB changes in more saline, drier valleys[1] -Moisture was positively correlated to fungi abundance while salinity was negatively correlated[2]	[1]Magalhaes et al 2014 [2]Arenz et al 2011
	Invertebrates	-*Scottnema* and *Plectus* are both negatively affected by salt, but type and concentration matter[1] -Populations of *Scottnema*, *Eudorylaimus*, and *Plectus* are negatively related to salinity[2]	[1]Nkem et al 2006 [2]Powers et al 1998
Communities			
	Microbes	-Community composition shifts with salinity (i.e. shift from Actinobacteria to Firmicutes dominated)[1,5] -Greater community diversity of microbes in drier soils[2] -Salinity is a significant driver of microbial communities across 4 valleys[3] -negative relationship between alpha diversity of microbial communities and salinity[4] -Soil moisture is a significant predictor of bacterial community diversity at the genus level[5]	[1]Van Horn et al 2014 [2]Takacs-Vesbach et al 2010 [3]Lee et al 2011 [4]Okie et al 2015 [5]Geyer et al 2014
	Invertebrates	-Greater invertebrate community diversity in less saline soils[1,2,3] -Greater invertebrate community diversity with higher soil moisture[1,2,3] -Community structure is influenced by soil moisture *Plectus* and *Eudorylaimus* are associated with wetter soils, *Scottnema* with drier[1,2,3,4]	[1]Nielsen et al 2011 [2]Ayres et al 2007 [3]Treonis et al 1999 [4.]Powers et al 1998
Ecosystem			
	Microbes	-Water tracks alter respiration rates, but depends on the soil chemistry, including salinity[2] -Lower microbial biomass in saltier, drier valleys[3] - Moisture addition did not affect microbial biomass in a field experiment[4] -Along with pH and organic carbon, salinity was one of the best predictors of microbial activity in soils of lake and stream margins[5]	[2]Ball and Virginia 2012 [3]Tampaari et al 2012 [4]Ball et al 2018 [5]Zeglin et al 2009
	Invertebrates	-Water tracks affect soil invertebrate habitats, but depends on soil chemistry, including salinity[1], and have been found to have lower invertebrate abundance, associated with higher salinity[3] -Salinity and moisture are significant drivers of habitat suitability for invertebrates, *S. lindsayae* is found in saltier, drier soils[2]	[1]Ball & Virginia 2012 [2]Courtright et al 2001 [3]Smith et al 2012

Table 3.2. Results of three-way ANOVA. Effects of community (C), moisture (M), and salinity (S) treatments on *Eudorylaimus* total abundance, *Scottnema* total abundance, *Scottnema* adults, *Scottnema* juveniles, *Scottnema* females, *Scottnema* males, total bacterial cells, fungal biomass (d.f. = degrees of freedom).

Effect	d.f.	F	p	Effect	d.f.	F	p
Eudorylaimus total abundance				*Scottnema* total abundance			
C	**1,32**	**19.89**	**<0.0001**	C	1,31	2.02	0.165
M	1,32	0.29	0.597	M	1,31	1.57	0.220
S	1,32	0.10	0.759	**S**	**1,31**	**6.25**	**0.018**
C*M	1,32	0.033	0.858	C*M	1,31	0.62	0.437
M*S	1,32	1.252	0.271	M*S	1,31	0.48	0.494
C*S	1,32	0.164	0.688	C*S	1,31	0.10	0.758
C*M*S	1,32	3.362	0.076	C*M*S	1,31	3.21	0.083
Scottnema adults				*Scottnema* juveniles			
C	1,35	0.82	0.371	C	1,31	1.46	0.237
M	**1,35**	**4.82**	**0. 035**	M	1,31	0.38	0.544
S	**1,35**	**8.47**	**0. 007**	**S**	**1,31**	**4.24**	**0.048**
C*M	1,35	0.195	0. 662	C*M	1,31	0.38	0.541
M*S	1,35	0.49	0.489	M*S	1,31	0.039	0.844
C*S	1,35	0.11	0.737	C*S	1,31	0.226	0.638
C*M*S	**1,35**	**5.75**	**0.023**	C*M*S	1,31	1.675	0.205
Scottnema females				*Scottnema* males			
C	1,31	3.60	0.067	C	1,31	0.35	0.5574
M	1,31	2.01	0.167	M	1,31	3.239	0.0817
S	**1,31**	**9.81**	**0.004**	S	1,31	2.023	0.1649
C*M	1,31	0.72	0.403	C*M	1,31	0.448	0.5085
M*S	1,31	1.49	0.232	M*S	1,31	0.677	0.4169
C*S	1,31	0.37	0.548	C*S	1,31	0.599	0.4450
C*M*S	1,31	3.38	0.076	C*M*S	1,31	3.436	0.0733
Bacteria cells							
C	**3,53**	**7.34**	**0.0003**				
M	1,53	0.35	0.557				
S	1,53	3.51	0.067				
C*M	3,53	0.75	0.527				
M*S	1,53	0.03	0.870				
C*S	**3,53**	**16.41**	**<0.0001**				
C*M*S	3,53	0.68	0.568				

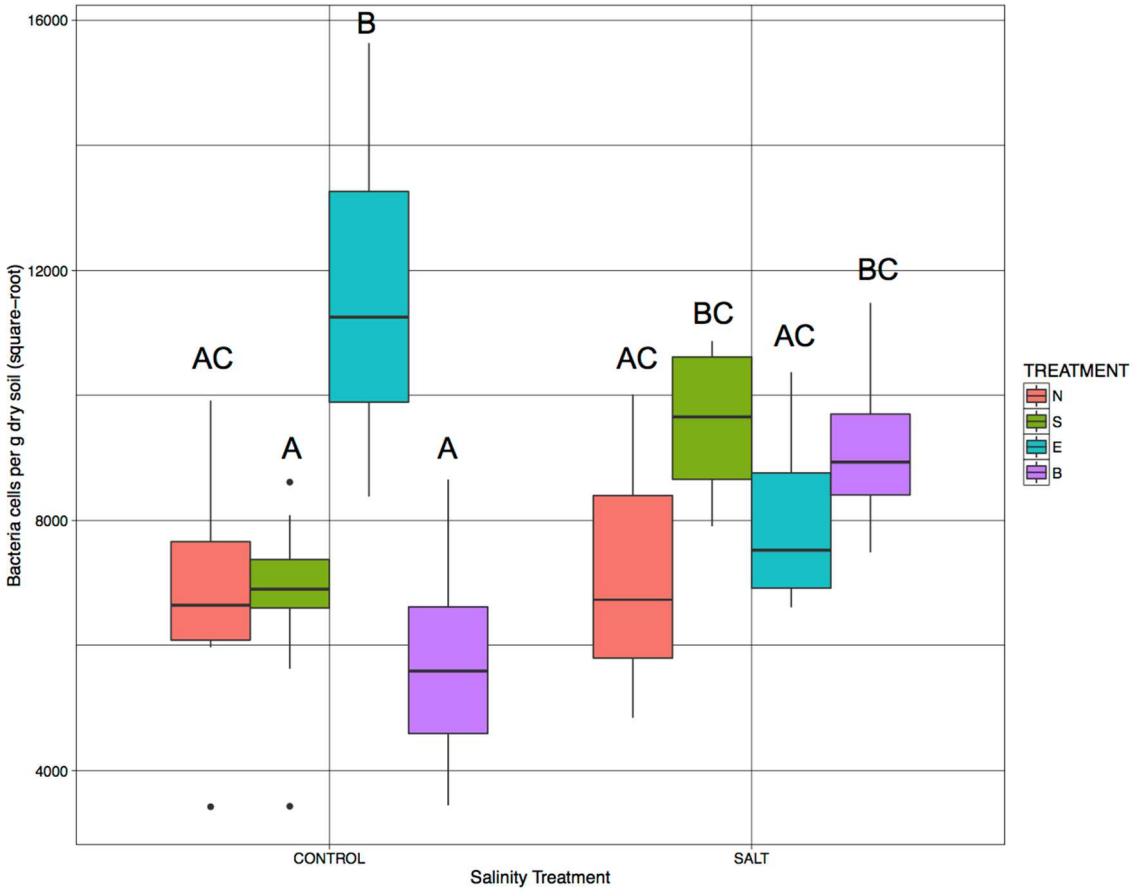
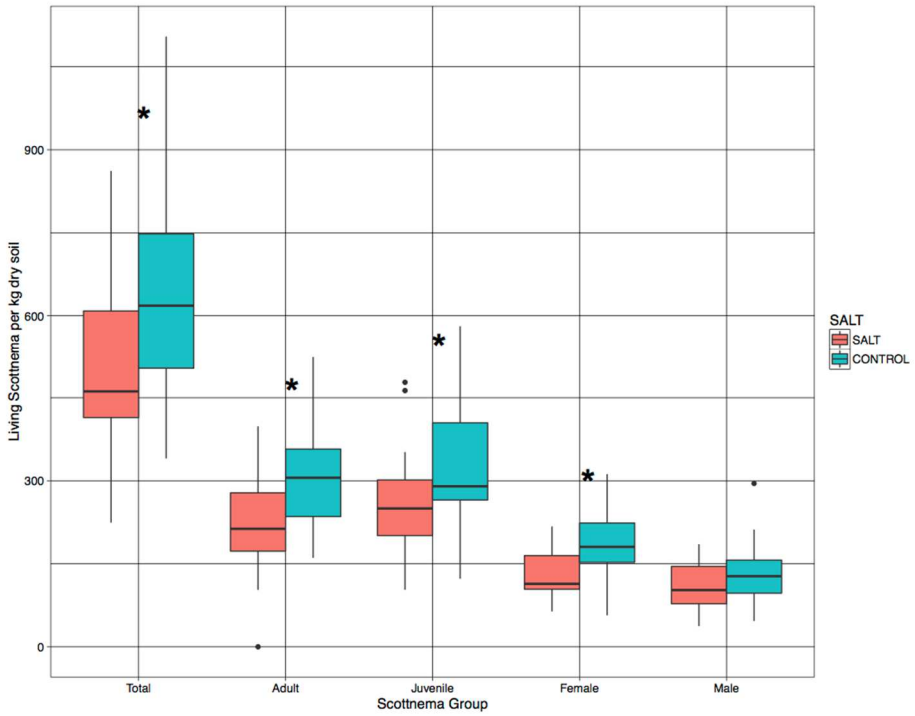


Figure 3.1: Community and salinity treatment effects on total bacterial cells. Treatments on the x-axis are Control salinity and High salinity. Colors correspond to community treatments: N= no nematodes (control), S= *Scottnema* only, E = *Eudorylaimus* only, B = Both *Scottnema* and *Eudorylaimus*. Different letters denote community treatments with significant differences ($p<0.05$, LSMeans).

A.



B.

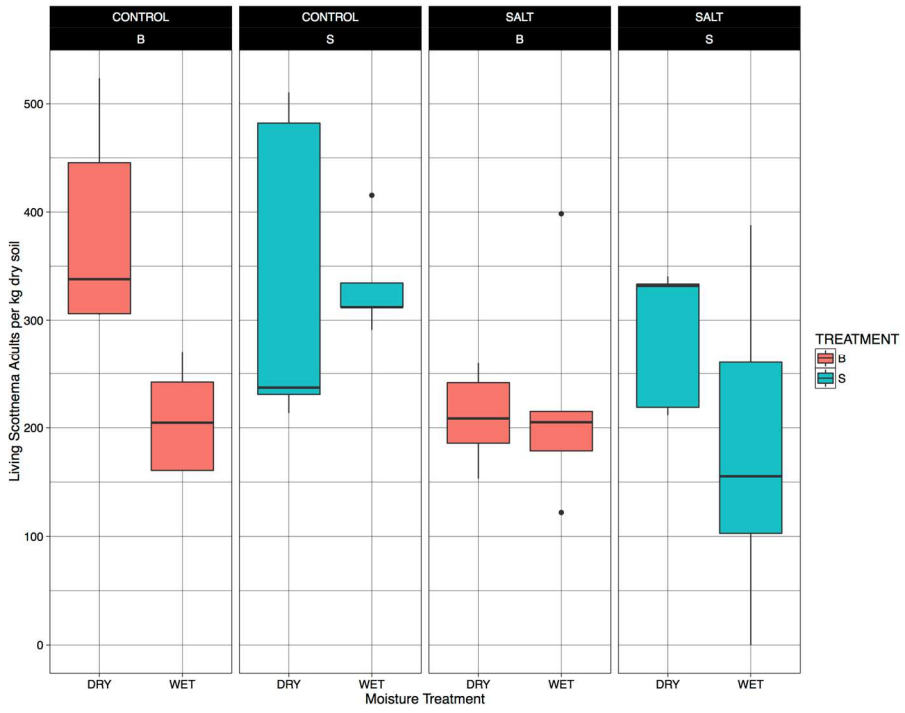


Figure 3.2: Salinity treatment effects on (A) total living, adult, juveniles, female, and male *Scottnema*. Asterisks denote significant differences ($p<0.05$) between salinity treatments, (B) Community*Salinity*Moisture effects on *Scottnema* adults, Community treatments are S= *Scottnema* and B = Both *Scottnema* and *Eudorylaimus.*

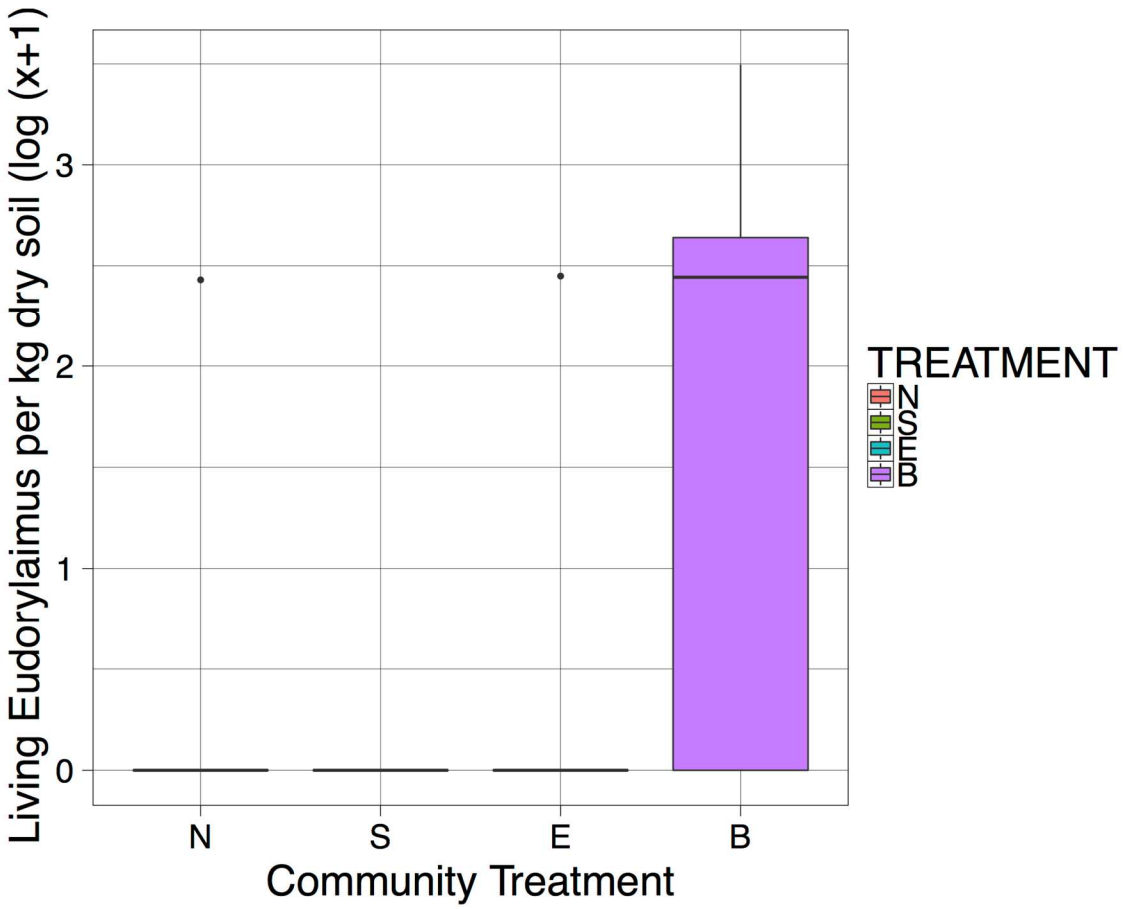


Figure 3.3: Effect of community treatment on total living *Eudorylaimus*. N= no nematodes (control), S= *Scottnema* only, E = *Eudorylaimus* only, B = Both *Scottnema* and *Eudorylaimus.*

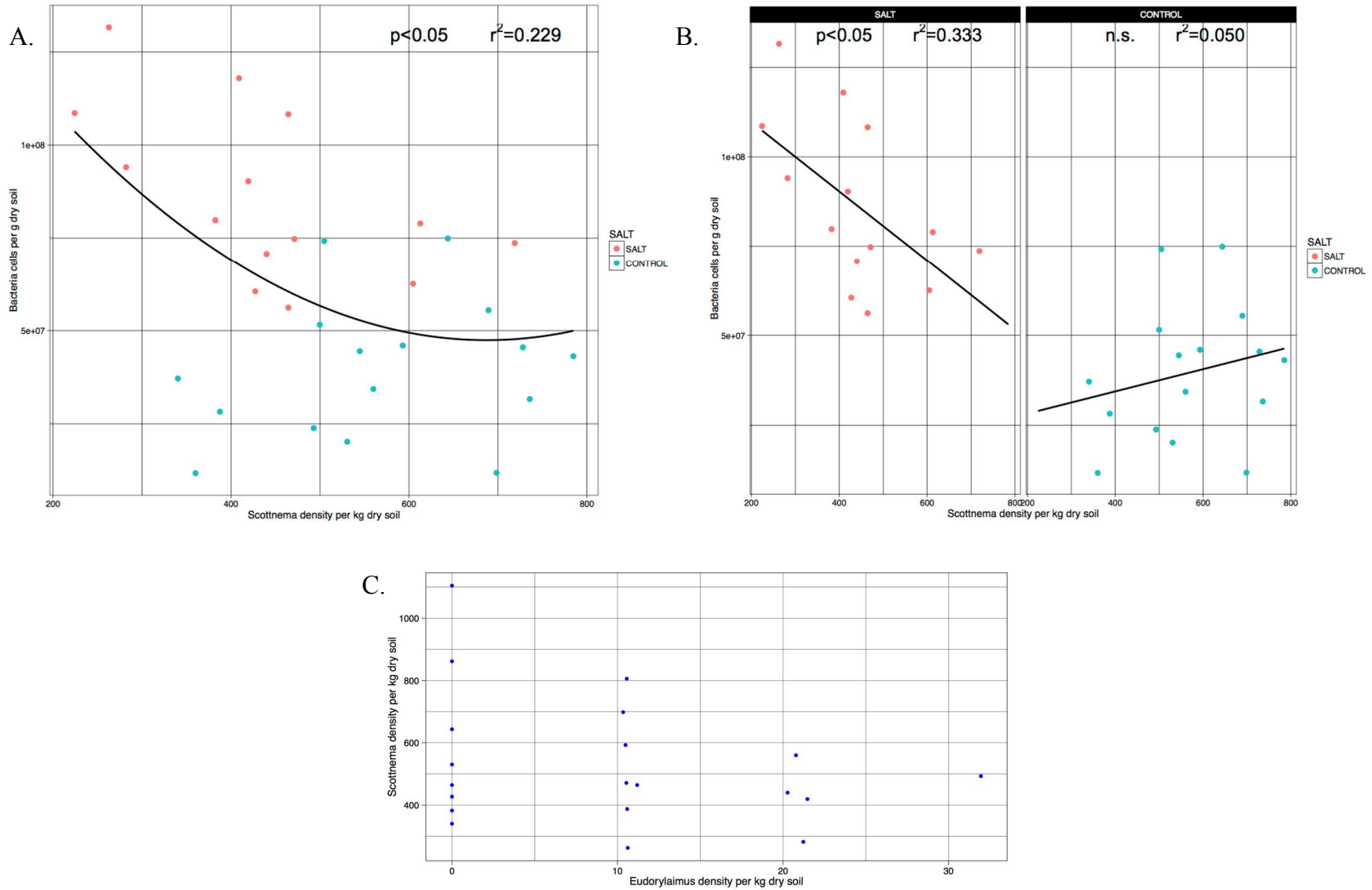


Figure 3.4: Relationship between (A) *Scottnema* and bacteria abundance overall, (B) *Scottnema* and bacteria abundance by salinity treatment, and (C) *Eudorylaimus* and *Scottnema* abundance

CHAPTER 4 – SOIL FOOD WEB COMPLEXITY VARIES WITH CARBON SOURCE ACROSS THE MCMURDO DRY VALLEYS

Summary

Despite extremely low organic carbon availability, the McMurdo Dry Valleys of Antarctica support a multi-level soil food web, including microbivore and omnivore-predator invertebrates. This challenges the classical understanding of food web structure, where such low resource availability is predicted to limit trophic complexity. Various combinations of soil fauna communities exist in the McMurdo Dry Valleys depending on habitat, resources, and geographic location, but it is unclear which organic carbon (C) sources fuel these food webs and if the soil food web structure varies with carbon source and availability. While soil organic C includes minor contemporary inputs from moss, cyanobacterial, or cryptoendolithic sources, additional sources include windblown detritus from modern cyanobacterial mats, marine detritus, and remnant ancient detritus from paleo-lakes. We asked: How do soil food webs vary across the landscape? We expected the trophic position of soil fauna to remain stable across the landscape, while complexity varied. Specifically, we hypothesized that food webs would have lowest complexity in the lowest productivity sites (high elevation) and highest in the most productive sites near the coast. We expected that paleo-lakes would impact soil food webs at low elevations and isotopic signatures would reflect C source. In a field study, we sampled both wet and dry habitats across 8 valleys. We then did an in-depth study of Taylor Valley to assess the potential impact of a paleo-lake on the soil food web. Results showed that C sources were identifiable with unique isotopic signatures and there were three distinct trophic levels in the soil food web. While isotopes revealed *Eudorylaimus* as an omnivore-predator in wet soils, its trophic position differed in dry soils, reflecting a switch to a primary consumer positions under low resource

availability. Furthermore, the isotopic signatures of *Scottnema* from the oldest soils (Taylor IV drift) were significantly lighter in ^{13}C than the younger dry soils, but this pattern was reversed in wet soil. This suggests that there is very old, highly processed soil organic matter in Taylor IV dry soils, which do not receive contemporary inputs from primary production as in wet habitats. This research reveals that Antarctic Dry Valley soil food webs are variable in their complexity and structure across the dry valleys landscape and with habitat.

Introduction

One of the oldest organizing concepts in ecology is the food web (Elton 1927). Food web structure and size varies in natural communities and repeatable patterns have been found in ecosystems around the world (Pimm 1982, Cohen and Briand 1984, Cohen et al. 2003). Food webs are limited by primary productivity and resource availability because energy is lost with each transfer up the food chain (Hutchinson 1959). Productivity is not the only control on food web complexity: disturbance and ecosystem size also play a role in determining the number of trophic levels, or food chain length (Post 2002a, Thompson and Townsend 2004, Takimoto et al. 2012). However, low productivity ecosystems still challenge our understanding of the drivers of food web structure. For example, arid regions often support highly complex food webs (Ayal 2007, Megías et al. 2011, Segoli et al. 2016), despite the once classic paradigm that abiotic conditions control the diversity and trophic complexity of deserts. Questions remain about whether cold deserts also exhibit complex food webs despite harsh conditions and low productivity.

The harshest terrestrial ecosystems on earth include the ice-free regions of Antarctica. The largest of these areas is the McMurdo Dry Valleys, where low temperatures and scarcity of

liquid water constrain the abundance and activity of terrestrial organisms. There are no vascular plants and the cryptogamic vegetation is sparsely distributed. Thus, the primary production by mosses, lichens, terrestrial cyanobacteria and algae, including the microbial communities that grow inside of rocks (i.e. cryptoendoliths), is very limited (Friedmann and Ocampo 1976, Friedmann 1982, Green et al. 1992, Schwarz et al. 1992, Pannewitz et al. 2003, Novis et al. 2007). Despite this, soil organic carbon is present throughout the dry valleys, even in extremely arid soils that lack any sign of primary productivity (Cameron et al. 1970). The concentrations of this soil organic matter are extremely low – among the lowest on earth – and average just 0.01–0.03% organic carbon by weight and 0.003% by total nitrogen by weight (Campbell and Claridge 1987). Yet, these soils respire heterotrophic CO_2 (Parsons et al. 2004, Ball et al. 2009) and support active soil food webs (Freckman and Virginia 1997, Treonis et al. 1999, Stevens and Hogg 2002, Cowan et al. 2010). Furthermore, the widespread distribution of the microbivore nematode, *Scottnema lindsayae*, throughout the McMurdo Dry Valleys (Freckman and Virginia 1997) demonstrates that the quality and quantity of soil organic matter is sufficient to support at least two trophic levels.

Which organic sources support McMurdo Dry Valley soil food webs, whether one source dominates or various sources occur, and how these sources vary with habitat is poorly understood. Potential sources include windblown detritus from the microbial mats of modern lakes and from cryptoendoliths (Parker et al. 1982, Elberling et al. 2006, Hopkins et al. 2006), marine detritus (Burkins et al. 2001), and ancient organic deposits from paleo-lakes (Burkins et al. 2001, Hendy 2004, Moorhead 2007). The wind transport of organic matter from productive sites to bare soils has been a longstanding explanation for soil organic matter accumulation in dry valley soils (Matsumoto et al. 1990, Wharton 1993). Lacustrine microbial mats and

cryptoendoliths are visibly eroded by wind (Parker et al. 1982) and organic matter has been found in aeolian collections (Hopkins et al. 2009). However, some of the organic compounds found in soil are not likely derived from modern lacustrine detritus and a possible source is relict organic matter from ancient glacial tills and glacial lake deposits (Matsumoto et al. 1990). The McMurdo Dry Valley landscape is heterogeneous and is composed of soils deposited from at least 4 glacial tills ranging in age from 12,000-3,700,000 years old (Burkins et al. 2000). Additionally, glacial meltwater collects at low elevation in Taylor Valley during climate warming (Doran et al. 1994). Glacial Lake Washburn was the last large paleolake in Taylor Valley and covered all of Taylor Valley to a depth of 300 m about 22,800–8500 yr BP (Doran et al. 1994). Buried algal mats exist throughout the dry valleys and range from 1900 and 26,000 ^{14}C years BP in age (Hopkins et al. 2009). While this organic matter is a potential source, there is currently no direct estimate of the quantity of ancient algal mats in the different valleys.

Organic C has an estimated turnover time of about 130 years in the dry valleys, but under optimal conditions, its turnover could be much shorter (Barrett et al. 2005). This indicates that paleo-lake inputs from about 22,800–8500 yr BP (Doran et al. 1994) are either used up or are not the only source present. Stable isotopes have been used to identify sources of organic matter in soils in ecosystems around the world. Following this logic, previous research has used $\delta^{15}N$ and $\delta^{13}C$ to explore the sources of soil organic matter in the McMurdo Dry Valleys. Burkins et al (2001) found that soils were generally depleted in both isotopes, with values from Taylor Valley low elevations that generally tracked signatures for lake-derived organic material while higher elevations indicated marine or endolithic inputs. Hopkins et al (2009) expanded on this work showing that organic materials become depleted during decomposition and that soils in Wright Valley have endolithic origins while Garwood Valley soils are mixtures of lake-derived organic

inputs and either moss or endolith. However, it is unclear how these carbon sources might affect the soil food web structure and function.

Soil food webs vary across the landscape, with more complex communities in wetter environments at lower elevations (i.e., lake or stream margins) and less complex communities in drier, higher elevation sites (Treonis et al. 1999, Ayres et al. 2007). Generally, two soil food webs are defined in the dry valleys: wet and dry (see Chapter 1 and 2). Briefly, *Scottnema lindsayae* dominates dry soils while the nematodes *Eudorylaimus antarcticus*, *Plectus murrayi*, along with rotifers and tardigrades prefer wetter soil (Treonis et al. 1999). The trophic position of each of these nematode species, rotifers, and tardigrades have been identified using stable isotopes for one site in Taylor Valley (Shaw et al. 2018, Chapter 2). However, soil community structure varies with edaphic characteristics (Powers et al. 1998) and it is unclear if the trophic structure is the same landscape-wide.

We asked: How do soil food webs vary in their complexity and structure across the valleys with soil habitat (wet/dry), soil age, and elevation (a proxy for productivity)? Does trophic position of individual species shift across the landscape with resource availability? We hypothesized that food webs would be most complex in wet soils where biodiversity is known to be highest. We expected trophic structure to be stable and for each taxa, if present, to remain in the same trophic level regardless of location. We expected that soil carbon source would be detectable in soil fauna due to fractionation that occurs when energy is transferred up trophic levels and would reflect the primary producers most prominently in wet habitats where they are conspicuous. If paleo-lakes affect the soil food web, we expected the isotopic signature at low elevations to differentiate from the isotopic signature of the same habitat at high elevations.

Methods

Study site and sampling scheme

To assess a broad scale elevation gradient, we collected 160 soil samples from across the McMurdo Dry Valleys landscape (specific locations with GPS coordinates are in Appendix 1). We selected sites along in 8 valleys from the coast to high elevation valleys near the polar plateau. The high elevation, low productivity valleys were Beacon, Wall, Virginia, and University and the low elevation, higher productivity valleys were Garwood, Taylor, Miers. Wright Valley was considered as a mid elevation valley. The high elevation valleys such as University and Beacon are known to be extremely cold and dry, among the harshest places for life (Goordial et al. 2016). In each valley, we aimed to collect 6 samples from two habitats: wet and dry (12 samples total). Wet habitats were within 3m of stream, lake or snowpack and had visibly moist soil. Dry sites were >5m from any stream or lake with no physical evidence of recent inundation. Due to the remoteness of the fieldwork and difficulty reaching these locations, these samples were collected over four years (see details in Appendix 1). Both habitat types were not always present in every valley. For example, Beacon, University, Wall, and Virginia Valleys have no streams or lakes and soil moisture is extremely low. Therefore, no wet habitats were sampled in these locations. Within Taylor Valley, we designed a more detailed sampling scheme to explore the effects of local factors on food web structure and to help to understand how differences in elevation might influence food webs. We chose sites in each lake basin (Lakes Fryxell, Hoare, and Bonney) as well as at the mouth of Taylor Valley near the Ross Sea (e.g Hjorth Hill) and high elevation ponds (e.g. Marr and Parera Ponds). Within each location, we collected samples from both wet and dry habitats. We also collected both high (>300m ASL, above paleo-lake bounds) and low elevation samples within each lake basin. Our samples were

collected in a range of glacial tills. Specifically, Hjorth Hill and Fryxell basin were in the Ross I drift (24,000–12,000 yr BP), Hoare basin samples and low elevation Bonney basin samples were taken in Taylor II/Bonney drift (98,000–74,000 yr BP) and high elevation Hoare samples were in Taylor III (200,000 – 210,000 yr BP), and the Upland Pond and high elevation Bonney samples (e.g. Andrew's Ridge) were in Taylor IV (2,100,000-3,700,000 yr BP).

Samples were collected with clean plastic scoops to 10 cm depth or to permafrost (whichever was reached first) and placed in sterile polyethylene Whirl-Pak bags. Coordinates for the location of each sample was recorded with a handheld GPS unit. All soils were kept in insulated coolers while in transit to the McMurdo Station laboratory facilities, where they were immediately placed into temporary storage at 4°C. Soil were slowly frozen by lowering the temperature to -20°C over 4 days (as in: Shaw et al. 2018). The soil was shipped frozen (-20°C) to Colorado State University, Fort Collins, Colorado, USA. At time of soil fauna extractions, we slowly defrosted the soils (as in: de Tomasel et al. 2013) before use.

Soil fauna extraction and identification

Nematodes, tardigrades, and rotifers were extracted from soils using sugar centrifugation procedures, modified to keep Antarctic soils and all extraction materials at a constant cold temperature (Freckman and Virginia 1993). Within 48 h of extraction, taxonomic groups were identified (nematodes identified to species and tardigrades and rotifers to phylum, Olympus CKX41, 200X magnification) and counted. At the time of extraction, a 10 to 20-g soil subsample was dried at 105°C for 48 h to determine gravimetric soil moisture (water mass per unit soil mass) by mass loss. All soil fauna counts were then adjusted for soil moisture content and expressed as number per kg of dry soil.

Soil fauna isotope analysis

The natural abundance of ^{13}C and ^{15}N of cryptogams (mosses and algae), nematodes (*Eudorylaimus, Scottnema, Plectus*), tardigrades, and rotifers were measured to assess trophic position (Bokhorst et al. 2007, Crotty et al. 2014). We sorted nematodes to species under microscope and handpicked approximately 100 individuals of each for isotope analysis. Rotifers and tardigrades were also separated for isotope analysis and were grouped by phylum. A small subsample of moss and algae was taken and assessed when present. All invertebrate individuals were collected into tin cups (8x5mm, Elemental Microanalysis BN/170056) using an eyelash tool (Superfine eyelash with handle, Ted Pella, Inc., Prod no. 113) for hand picking (as in: Shaw et al. 2016). For each taxon identified at each site, we aimed to triplicate fauna collections for isotope analysis. Extractions from 100 g of soil were repeated by site until sufficient biomass was achieved for each group found at that site. Note that at each site not all groups were present or lacked sufficient abundance to collect enough biomass for isotope analysis.

Data analysis

All isotope ratios are expressed in delta notation (δ) as a part per mil (‰) relative to a standard. Nitrogen is expressed as:

$$\delta^{15}N=[(^{15}N/^{14}N_{(sample)}-{}^{15}N/^{14}N_{(atmosphere\ N)}) \div (\ ^{15}N/^{14}N_{(atmosphere\ N)}) \times 1000$$

and carbon is expressed as:

$$\delta^{13}C=[(^{13}C/^{12}C_{(sample)}-{}^{13}C/^{12}C_{(PDB)}) \div (^{13}C/^{12}C_{(PDB)}) \times 1000$$

where atmospheric N is and PeeDee belemnite (PBD) are used as standards for N and C, respectively. Using isotopic mixing models (Phillips and Koch 2002), we determined trophic position and feeding preference for each of the invertebrate groups at each sample site.

Then, trophic complexity was measured as connectance and link density (Ulanowicz et al. 2014). Specifically, the number possible directional links in the McMurdo Dry Valley food web was counted (see food web schematic, Appendix 2), and link density (*LD*) was calculated as:

$$LD = \frac{L}{S}$$

and connectance (*C)* was then calculated as:

$$C = \frac{L}{S((S-1)/2)}$$

where *L* is the total number of directional links and *S* is the number of species present (van Altena et al. 2016). The number of species present at each site was used to assess richness. Abundance of organisms was used as a proxy for biomass present in a food web.

We mapped species abundance and diversity in R using packages maptools and rgdal. Briefly, Shapefiles for the Antarctic coastline, glaciers, streams and lakes were stacked. Then, our sampling sites were projected as points using latitude and longitude of sample location. Increasing circle size represented greater total fauna abundance, and increasing color warmth represented greater species richness.

Two-way ANOVAs were used to test for differences in food web connectance, link density, richness, and total soil fauna abundance between location and habitat across all valleys and all samples. For Taylor Valley, we used a mixed effects model to test if habitat and elevation affect total food web connectance, link density, richness, total soil fauna abundance, *Scottnema* abundance, *Eudorylaimus* abundance, *Plectus* abundance, Rotifer abundance, and Tardigrade abundance. Habitat (wet/dry) and elevation (high/low) were fixed effects with location within Taylor Valley as a random effect. We used post hoc tests (Tukey HSD) to confirm genuine

significant effects ($p < 0.05$). Residuals were tested for normality of distributions via Q-Q plots and Shapiro-Wilks tests, and data were log (x+1) if they failed (rejected when Shapiro-Wilks $p<0.05$). All data were transformed to log (x+1) for analysis. All analyses were performed in R (R-Core-Team 2014).

Results

Effects of habitat, valley location, and elevation on soil fauna and their food webs

The abundance and diversity of soil fauna varied across the dry valleys and differed by habitat (Table 4.1). There were significant main effects of habitat and valley location on food web complexity (connectance and link density), species richness, and total soil fauna abundance (Table 4.2). Generally, there was greater abundance and diversity in Garwood and Taylor Valleys, followed by Miers, Wright, Wall, University, Beacon, and Virginia (Fig 4.1). However, this diversity and food web complexity varied with habitat and location (Habitat*Location interaction, Table 4.2), where there was greater abundance of soil fauna in wet habitats in Garwood Valley and in low elevation sites in Taylor Valley, but in valleys farther from the coast and higher in elevation, there were less fauna in wet habitats and more found in dry habitats (Table 4.1). In the high elevation valleys (Beacon, University, Wall, and Virginia) diversity was very limited. No living fauna were found in Virginia Valley, while University Valley only contained rotifers (Table 4.1). Tardigrades and rotifers were present at one site in Beacon Valley, along with a single living *Scottnema*. One site in Wall Valley had abundant *Scottnema* and tardigrades. In other locations, species diversity was generally greater.

Within Taylor Valley, there was a significant main effect of habitat on foodweb connectance, link density, richness, as well as *Scottnema*, *Plectus*, rotifers, and tardigrades

(Table 4.3). Diversity, and thus, food web complexity, was greatest in wet soils. Only *Scottnema* was less abundant in wet habitat (Table 4.1). Additionally, there was a significant interactive effect of habitat and elevation on *Eudorylaimus*, *Plectus*, and tardigrades (Table 4.3). While these groups were more abundant in wet habitat at low elevation, at high elevation the effect of moisture on their abundance was not significant. The greatest density and diversity of soil fauna was at the low elevation, wet site at Lake Fryxell (Fig 4.1).

Primary producers in the McMurdo Dry Valleys vary in their isotopic composition (Fig 4.2). Lake and stream mats have a consistent $\delta^{15}N$ of 2.67±0.86, but vary from -24.99 to -4.42 in $\delta^{13}C$. On the other hand, mosses and endoliths have a consistent $\delta^{13}C$ of -26.98±4.95 but vary widely in their $\delta^{15}N$ (Fig 4.2). Endoliths and the mosses from Garwood and Miers are depleted in $\delta^{15}N$, while Hjorth mosses along with the microbial mats are more enriched (Fig 4.2). The primary producers were enriched relative to the soil organic matter (Fig 4.3 and 4.4), and similarly, a dried mat above the shoreline at Lake Fryxell was also depleted compared nearby active mats (see Fig 4.2b; Lawson et al. 2004). To assess the state of organic matter decomposition, we measured the $\delta^{13}C$ and $\delta^{15}N$ for a primary consumer, *Scottnema*, by soil age and habitat. We found that in dry habitat (vs. wet habitat), *Scottnema* biomass was significantly depleted in $\delta^{13}C$ and $\delta^{15}N$ with soil age, and was lightest in the oldest soil, the Taylor IV drift (Fig 4.5). However, *Scottnema* in wet habitat did not significantly differ in isotopic composition by soil age (Fig 4.5).

In wet habitats, where primary productivity was evident, the soil food webs derived energy directly from the primary producers and were more enriched in $\delta^{15}N$ and $\delta^{13}C$ relative to the source (e.g. Fryxell wet, Bonney wet, and wet and dry in Garwood, Fig 4.4b and 4.4e, Fig 4.3d, respectively). When food webs were detrital, soil fauna were depleted in $\delta^{13}C$ relative to

the source, but $\delta^{15}N$ values varied. For example, in Wall Valley (Fig 4.3a) the nematodes and tardigrades tracked endolith-derived organic matter. The trophic positions of soil fauna are well conserved across wet habitats, but varied in dry habitats (Fig 4.3 and 4.4), where *Plectus*, rotifers, and tardigrades are primary consumers in wet habitats, with *Eudorylaimus* at the top of the food web. In dry habitats, (particularly Miers Valley, Wright Valley, Lake Hoare low elevation, and Lake Fryxell) *Scottnema*, a primary consumer, has a very similar or even heavier isotopic signature than *Eudorylaimus* (Fig 4.3c,e and Fig 4.4b-c). However, *Eudorylaimus* is in the top trophic position in Bonney dry habitats at low elevation soils (Fig 4.4e) and Lake Hoare dry habitats at high elevation (Fig 4.4c).

Discussion

Soil food web complexity and structure varies with habitat

As 'McMurdo's equivalent of elephants and tigers'(Wilson 2002), the soil fauna are the top consumers and predators in this food web. Until recently, no top-down effects had been found (but see Chapter2 1 and 2) and all factors affecting soil communities were assumed to be abiotic (Hogg et al. 2006). Even so, abiotic factors such as water, temperature, salinity, and pH are known to limit life in Antarctic soils (Courtright et al. 2001, Poage et al. 2008), while the role of biotic interactions in structuring natural communities is still uncertain. As expected, soil food webs were most complex in wet habitats in the lowest elevations (e.g. Garwood and Taylor Valleys). This is similar to recent findings of Andriuzzi et al. (2018), who found that invertebrate diversity (Pielou's E) was greater in Garwood Valley compared to Taylor, but not Miers Valley. Furthermore, we found that food web complexity, measured as connectance and link density, decreased with distance from coast and elevation. This supports previous findings of soil fauna distributions (Adams et al. 2014), and suggests that complexity is tied to environmental factors

that may also play a role in primary productivity (Geyer et al. 2017). Within Taylor Valley at high elevations, wet communities were not significantly more diverse and abundant than the dry communities, suggesting that a factor besides moisture is limiting their diversity.

We hypothesized that food web structure would be stable, i.e. that soil fauna taxa would remain in the same trophic level whenever they were present at a site. However, food web structure was not conserved across habitats: *Eudorylaimus* was predominantly an omnivore-predator in wet habitats and a primary consumer in dry habitats (with a few exceptions, Fig 4.3 and 4.4). This finding, though counterintuitive, could be explained by resource quality and *Eudorylaimus'* role as an omnivore. When a shared resource for which two species compete becomes enriched, omnivores often switch to predation on their competitor (Diehl and Feissel 2001). Thus in low resource environments, omnivores remain as competitors, but in high resource environments, omnivores become more predatory (Diehl and Feissel 2001). As greater moisture across the landscape is predicted for the future (Gooseff et al. 2011, Fountain et al. 2014), which is likely to affect the extent of primary production, a potential shift in trophic positions has consequences for ecosystem functioning and community structure (Woodward et al. 2008).

Primary productivity and decomposition in the McMurdo Dry Valleys

Mosses and endoliths exhibit $\delta^{13}C$ values of -26.98 ± 4.95, typical of C3 photosynthesis (Fig 4.2), but stream and lake microbial mats vary in $\delta^{13}C$. The fractionation associated with CO_2 concentration in frozen, aquatic or temporally aquatic environments contributes to higher $\delta^{13}C$ in mat biomass (Lawson et al. 2004). The relatively heavy $\delta^{15}N$ of the mats (2.67 ± 0.86) suggests biological N fixation (Delwiche et al. 1979), while the lighter values of endoliths and mosses are derived from atmospheric N deposition. The relatively higher $\delta^{15}N$ of the mosses at Hjorth Hill

(Fig 4.2) compared to the mosses from Miers and Garwood can be attributed to marine aerosols, which have a heavier isotopic signature than N from atmospheric deposition (Burkins et al. 2000).

Soil organic matter in the McMurdo Dry Valleys becomes lighter ($\delta^{13}C$, $\delta^{15}N$) during decomposition (Fig 4.3 and 4.4). This could be a result of structural components (biopolymers) in endoliths and mosses, that are not present in microbial mats and remain after preferable sources are used up (Matsumoto et al. 1990, Hopkins et al. 2009). These structural components are typically lighter in ^{13}C and ^{15}N than other components. Hopkins et al (2009) showed that organic matter become more depleted in ^{13}C during an incubation experiment and suggest that this could account for the light isotopic signatures of soils in the dry valleys. Similarly, Lawson et al (2004) found that dried lake mats decreased in $\delta^{13}C$ at increments from the shore, suggesting that older, more decomposed mats are more depleted.

We hypothesized that the primary consumers would reflect their sources and thus, those from older soils would have a lighter $\delta^{13}C$ signature relative to younger soils, reflecting more degraded organic materials. The isotopic signature of *Scottnema* from dry habitats became more negative in older soils, and was lightest in the oldest soil (Taylor IV, 2,100,000-3,700,000 yr BP). Furthermore, very light isotopic signatures indicate a lack of new organic input into the system, suggesting that residual carbon is very old. However, *Scottnema* from wet habitats did not track this depletion and there was no difference between young and old soils. Thus, we expect that even in very old soils, new moisture is linked to new carbon sources through primary production, which alleviate the isotope depletion and are quickly incorporated into the soil food web (see supplementary study, Appendix 2).

Overall, our study shows that trophic structure, complexity and diversity of soil invertebrate communities varies across the McMurdo Dry Valleys with habitat, elevation, and soil age. We have demonstrated that the organic sources that fuel these soil communities also vary, and that oldest soils receive very little input from contemporary sources. Furthermore, our results inform understanding of potential trophic interactions, which depend on the resource availability that varies from dry to wet habitat. Specifically, *Eudorylaimus'* trophic position differs from a predator in wet habitat and a competitor (potential predator) in dry habitat. As hydrological connectivity increases across the landscape and resource availability changes with climate change, we predict that increased primary productivity will drive greater organic carbon availability in formerly dry habitat and subsequently, the relative importance of predator-prey interactions will increase.

Table 4.1. Mean values of species richness, total fauna abundance, and nematode, rotifer, and tardigrade abundance (±standard error). Sample locations are organized by increasing distance from coast/elevation.

	Species Richness	Total Abundance	Nematodes			Rotifers	Tardigrades
			Scottnema	*Eudorylaimus*	*Plectus*		
Garwood Valley							
Dry	1.82±0.38	992±278	590±192	86±28	0±0	4±3	8±7
Wet	4.18±0.46	4318±1622	388±157	689±171	183±102	1816±1154	1026±433
Miers Valley							
Dry	2.0±0.0	2875±1642	1796±970	55±45	0±0	0±0	0±0
Wet	2.80±0.37	757±279	187±741	297±210	8±6	71±42	2±1
Taylor Valley							
Low elevation: (<100m ASL)							
Hjorth Hill							
Wet	4.25±0.25	1983±811	47±21	332±177	1107±634	265±114	21±21
Lake Fryxell							
Dry	1.00±0.00	557±409	13±9	0±0	0±0	0±0	0±0
Wet	5.00±0.00	6993±937	0±0	2145±640	326±128	2599±734	1091±341
Lake Bonney							
Dry	1.00±1.00	428±428	216±216	10±10	0±0	0±0	0±0
Wet	3.00±1.00	2748±2074	0±0	66±56	95±95	2121±2121	56±56
High elevation: (>100m ASL)							
Lake Fryxell							
Dry	1.71±0.29	1369±681	899±462	25±12	0.0±0.0	0.0±0.0	0.0±0.0
Lake Hoare							
Dry	1.8±0.37	3210±1917	494±126	6±4	4±4	0±0	0±0
Wet	6	1040	235	55	22	165	330
Upland Ponds							
Dry	1.00±0.46	1518±958	1276±909	5±4	0±0	152±134	0±0
Wet	3.25±0.37	1469±498	0±0	0±0	232±182	1074±526	86±42
Lake Bonney							
Dry	1.2±0.49	1976±1272	1012±738	0±0	0±0	4±2	0±0
Wet	1.67±1.67	607±602	277±277	42±42	3±3	0±0	66±66
Wright Valley							
Dais *(Dry)*	1.50±0.19	1047±273	460±171	19±14	0±0	0±0	1.25±1.25
Vanda *(Dry)*	0±0	0±0	0±0	0±0	0±0	0±0	0±0
Brownworth *(Wet)*	0.25±0.25	163±163	91±91	9.25±9.25	0±0	0±0	0±0
Wall Valley	0.38±0.26	914±913	30±30	0±0	0±0	0±0	783±783
Virginia Valley	0.13±0.13	1.25±1.25	0±0	0±0	0±0	0±0	0±0
Beacon Valley	0.24±0.14	431±253	0.59±0.59	0±0	0±0	430±253	0±0
University Valley	0.45±0.21	220±125	0±0	0±0	0±0	216±124	3±2

Increasing distance from coast and increasing elevation ↓

Table 4.2. Results of two-way ANOVA. Effects of location (L) and habitat (H) and their interaction (L*H) on food web connectance, trophic link density, diversity, and total soil fauna abundance (d.f. = degrees of freedom). Significance was accepted at alpha<0.05 and is denoted by (*).

Effect	d.f.	F	p	Effect	d.f.	F	p
Trophic link density				Food web connectance			
L	14,133	18.14	**<0.0001***	L	14,133	17.74	**<0.0001***
H	1,133	57.06	**<0.0001***	H	1,133	63.04	**<0.0001***
L*H	4,133	2.57	**0.041***	L*H	4,133	2.93	**0.023***
Species richness				Soil fauna abundance			
L	14, 133	16.795	**<0.0001***	L	14,133	11.42	**<0.0001***
H	1,133	42.87	**<0.0001***	H	1,133	13.17	**0.0004***
L*H	4,133	1.848	0.123	L*H	4,133	2.01	0.097

Table 4.3. Results of mixed effects models. With location in Taylor Valley as a random effect, the effects of habitat (H) and elevation (E) on food web connectance, link density, diversity, total soil fauna abundance, *Scottnema* abundance, *Eudorylaimus* abundance, *Plectus* abundance, rotifer abundance, and tardigrade abundance (d.f. = degrees of freedom, t = t-value, p=p value). Significance was accepted at alpha<0.05 and is denoted by (*).

Effect	d.f.	t	p	Effect	d.f.	t	p
Trophic link density				Food web connectance			
E	38	-0.72	0.473	E	38	-0.72	0.473
H	38	3.18	**0.003**	H	38	3.18	**0.003***
E*H	38	2.38	**0.022**	E*H	38	2.38	**0.022***
Species richness				Soil fauna abundance			
E	38	-0.65	0.522	E	38	-0.39	0.697
H	38	4.03	**0.0002***	H	38	0.10	0.921
E*H	38	1.66	0.104	E*H	38	1.57	0.123
Scottnema				Eudorylaimus			
E	38	-1.73	0.090	E	38	-0.92	0.365
H	38	-2.68	**0.010***	H	38	0.11	0.913
E*H	38	0.54	0.587	E*H	38	4.87	<**0.0001***
Plectus				Rotifers			
E	38	0.04	0.9679	E	38	-0.30	0.764
H	38	3.48	**0.001***	H	38	2.69	**0.010***
E*H	38	2.89	**0.006***	E*H	38	2.31	**0.026***
Tardigrades							
E	38	-0.18	0.860				
H	38	3.58	**0.001***				
E*H	38	1.62	0.111				

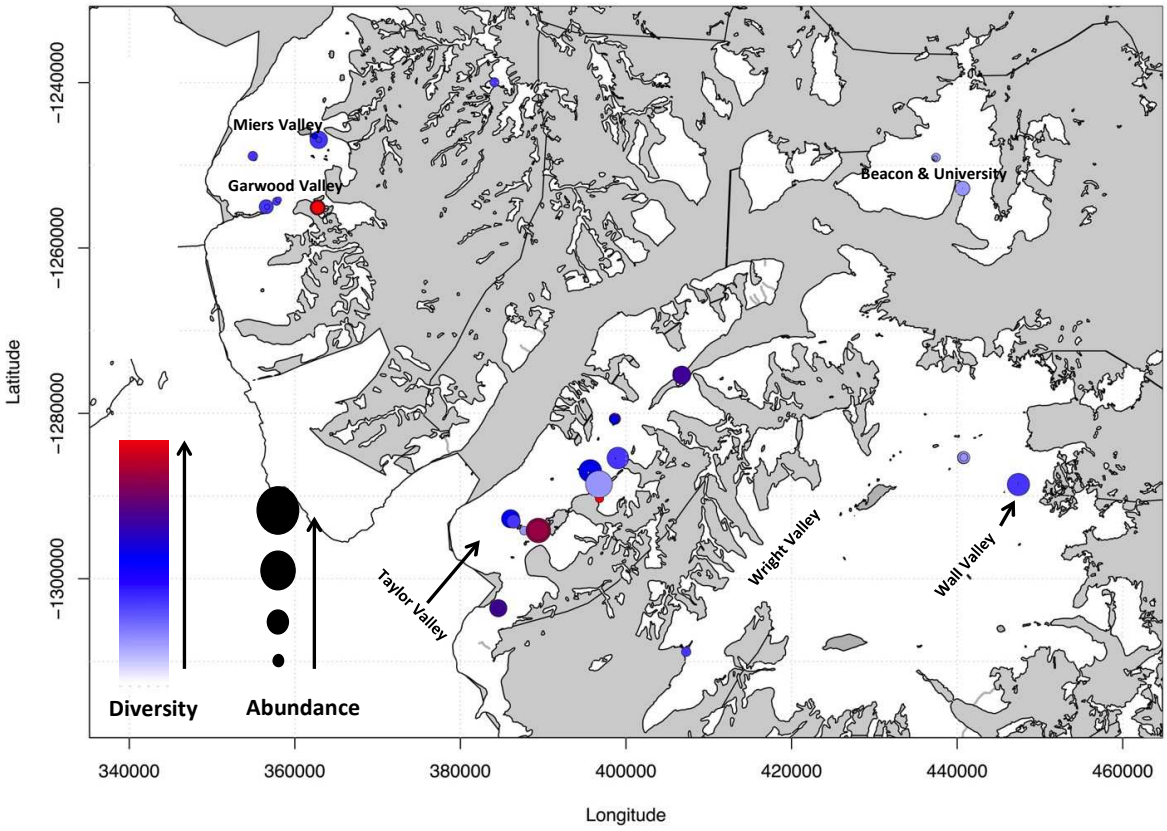


Figure 4.1. Map of the dry valleys showing soil fauna abundance and diversity by location. Circle size increases with increasing abundance of soil fauna. Colors indicate low (blue) to high (red) diversity (number of species). Other features (glaciers, streams, and lakes) are shown in gray.

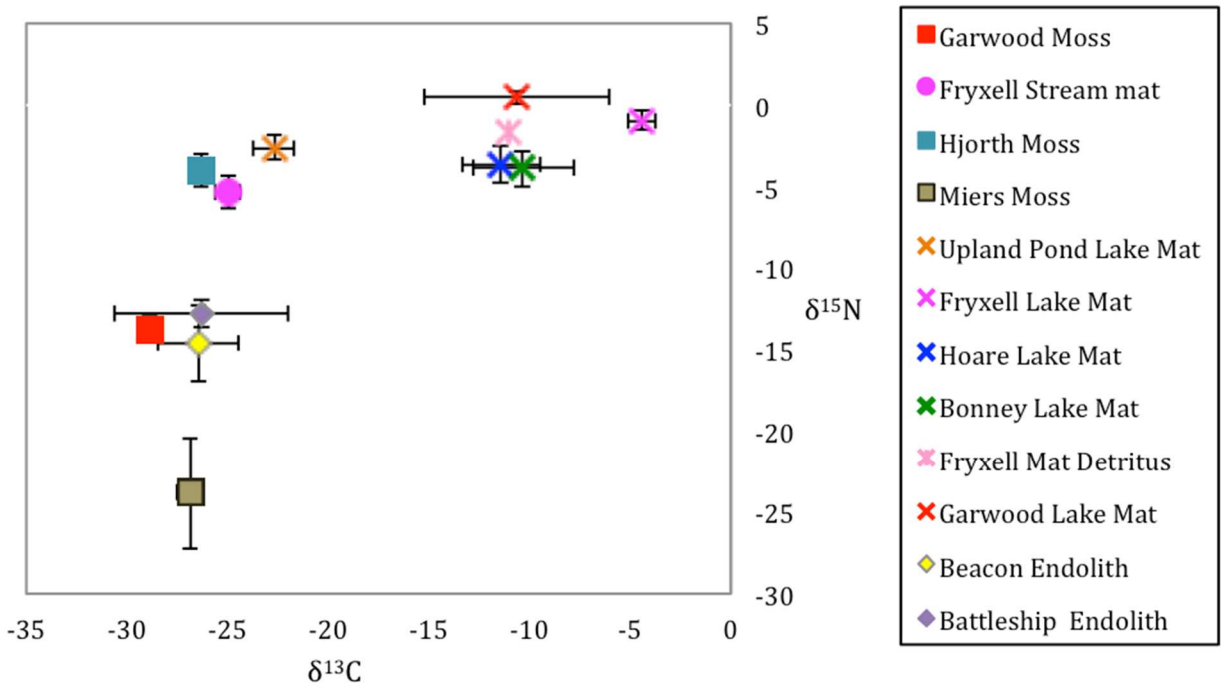


Figure 4.2. Comparison of the stable isotope composition of primary producers. Lake mats are denoted with an X, stream mats with a circle, mosses with a square, and endoliths with a diamond. All lake mat data except Garwood are from Lawson et al. (2004). Battleship endolith and Garwood lake mat data are from Hopkins et al (2009). Beacon endolith data are from Burkins et al (2001). All other data from this study. All mats shown here were active (wet) when sampled, except Fryxell Mat Detritus, which was a dried mat >1m from the lake shore.

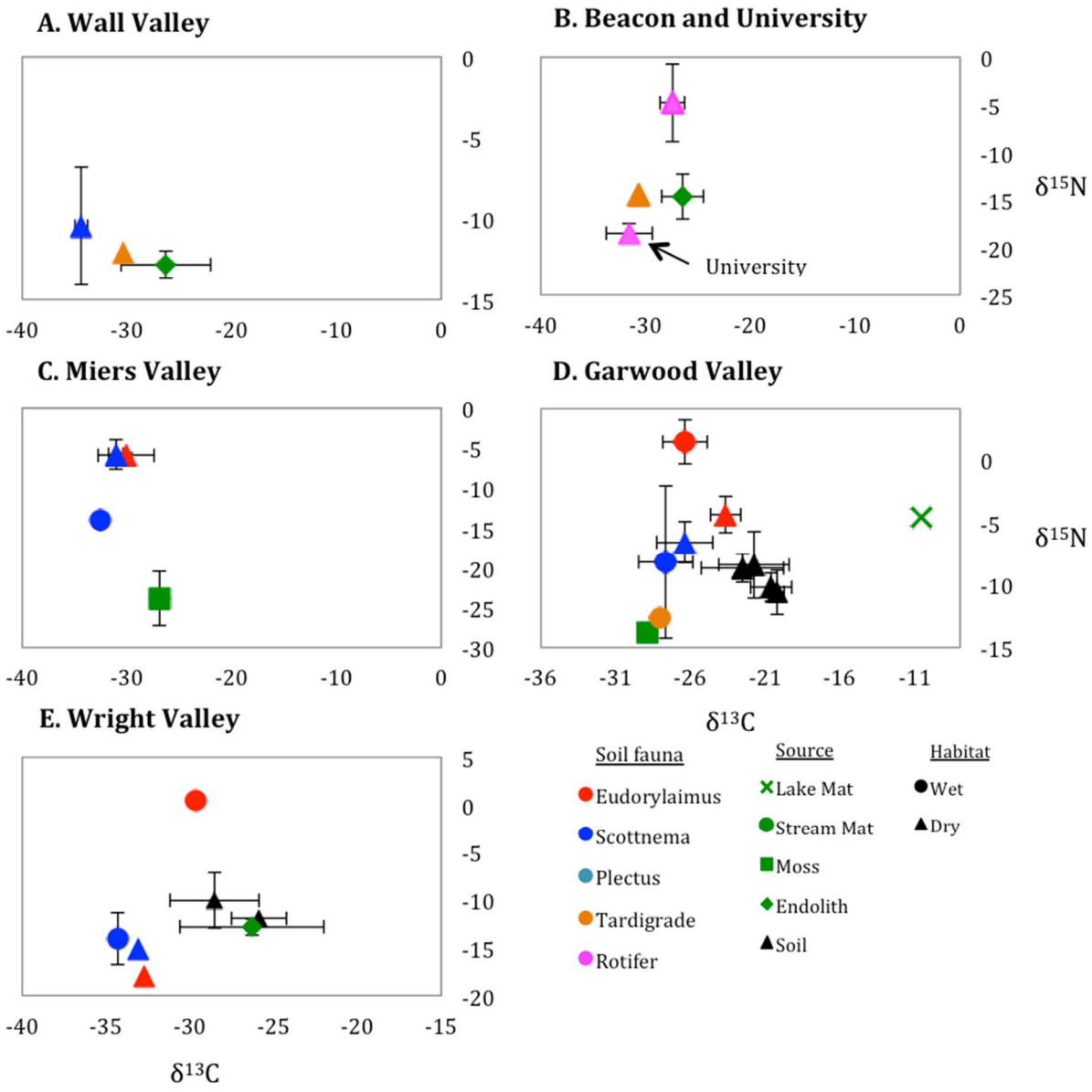


Figure 4.3. δ13C and δ15N values for soil fauna, soil, and organic sources for high elevation valleys (A, B), coastal valleys (C, D), and an intermediate valley (E). Colors denote fauna groups. All primary producers are green, but have different shapes. Soil is a black triangle. Shapes show habitat (circles=wet and triangles=dry). Endolith values shown in plot A and E and Garwood soils in plot D are from Hopkins et al 2009. Beacon endolith values shown in plot B are from (Burkins et al. 2000). All others are from this study. All mats shown here were active (wet) when sampled.

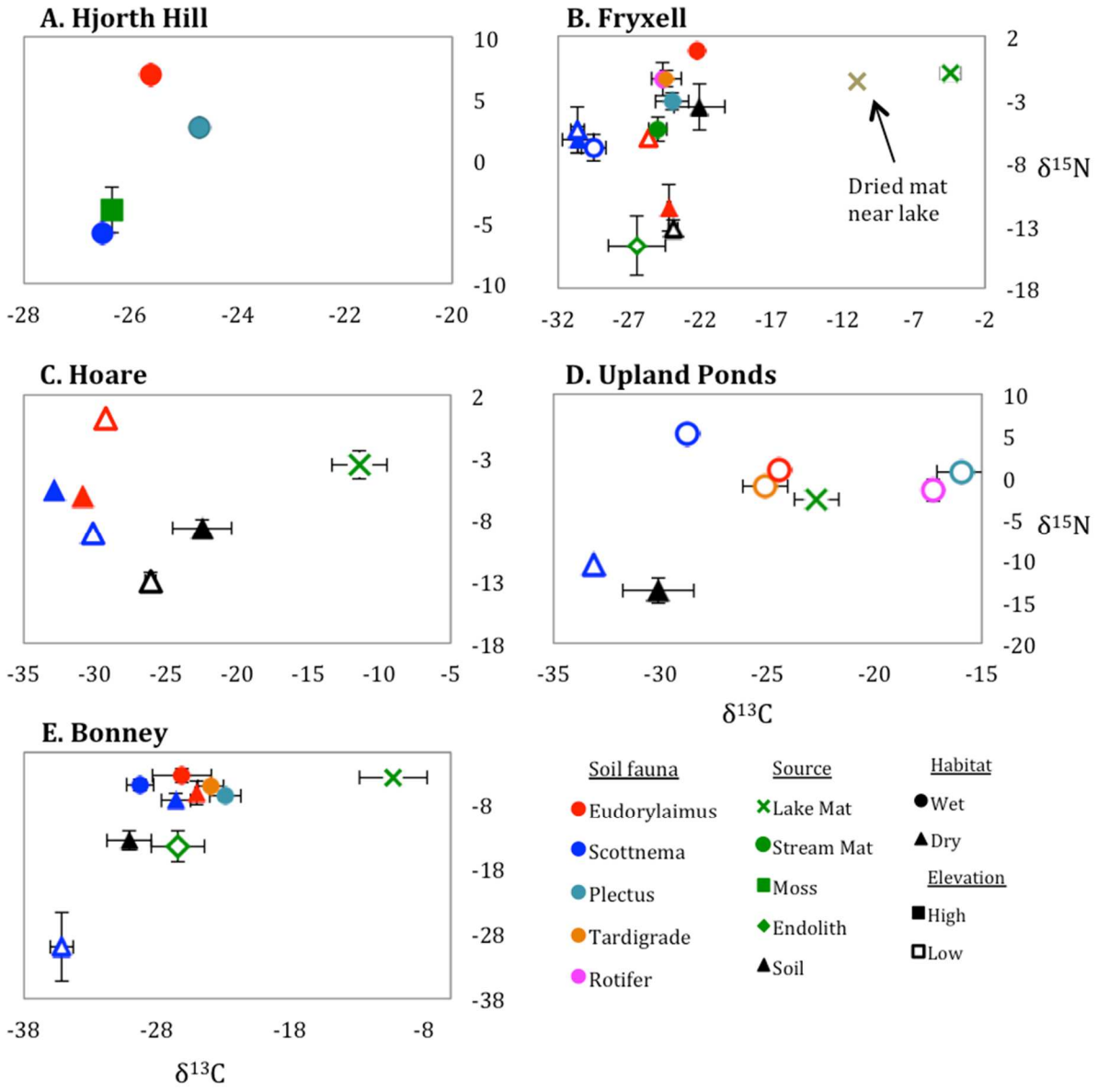


Figure 4.4. δ13C and δ15N values for soil fauna, soil, and organic sources for locations in Taylor Valley. Colors denote fauna groups. All primary producers are green, but have different shapes. Soil is a black triangle. Shapes show habitat (circles=wet and triangles=dry). Empty shapes are from high elevation and filled shapes are from low elevation sites. Lake mat values shown in plot B, C, D, and E are from (Lawson et al. 2004). Endolith values shown in plot B and E, and soil values shown in B, C, D, and E are from (Burkins et al. 2000). All others are from this study. All mats were active (wet) when sampled, except one dried mat sampled near Lake Fryxell (B).

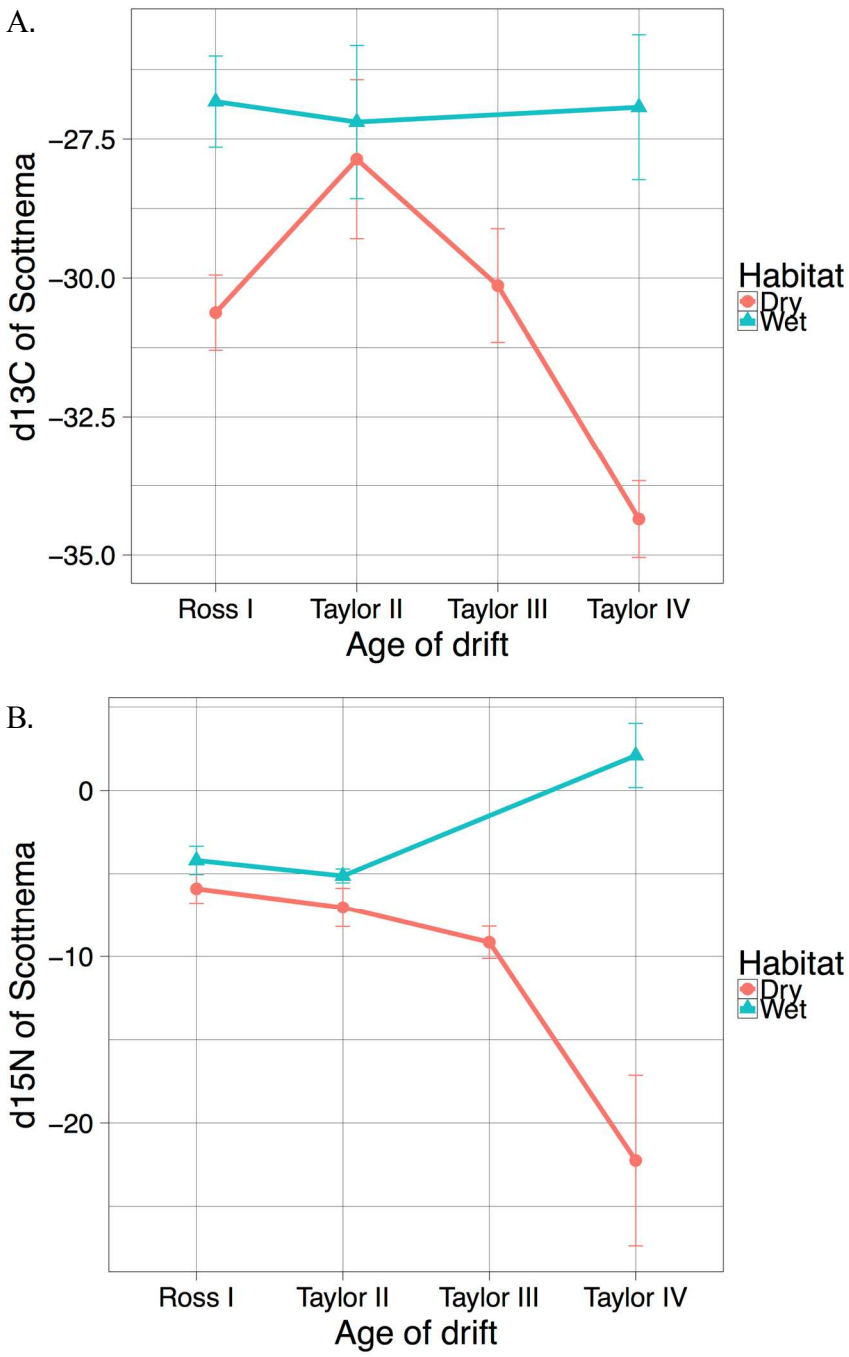


Figure 4.5. Mean natural abundance of (A) $\delta^{13}C$ and (B) $\delta^{15}N$ of the primary consumer, *Scottnema*, by soil age and habitat (±standard error) in Taylor Valley.

CHAPTER 5 – NITROGEN ADDITION AFFECTS THE SOIL NEMATODE COMMUNITY STRUCTURE AND SUCCESSIONAL MATURITY IN A SUBALPINE FOREST

Summary

Nitrogen deposition from anthropogenic sources is a global problem that reaches even the most remote ecosystems. Ecosystem responses belowground vary by ecosystem, and have feedbacks to geochemical processes, including carbon storage. A long-term nitrogen addition study in a subalpine forest has shown carbon loss over time, atypical for a forest ecosystem. Loss of microbial biomass is likely linked to lower soil carbon, but the mechanism behind this is still unknown. One possible explanation is through increased turnover due to grazing by soil fauna. Because nematodes occupy many trophic levels and are sensitive to trophic and environmental changes, assessing their communities helps to reveal belowground responses. In this study, we tested the hypothesis that long-term nitrogen fertilization affects nematode community structure and maturity beneath coniferous forests in the Rocky Mountains, indicating a faster cycling, bacterial driven system. We identified and enumerated nematodes by trophic group and family from experimental plots. Total nematode abundance was greater in fertilized plots compared to the control, but richness, diversity, and ecological maturity were lower. Nonmetric multidimensional scaling of the relative abundance of nematode families demonstrated that nematode community composition differed between treatments, driven by opportunistic bacterivores (e.g. Rhabditidae) in the fertilized plots and long-lived omnivores and predators in the control (e.g. Aporcelaimidae). Nematode maturity indices showed the nematode food web was enriched (indicating high nutrient/resource status) and structured (all trophic levels, including long-lived predators present) in both treatments, but significantly more enriched in the fertilized. The mechanism of this aboveground–belowground link between nitrogen deposition

and nematode community composition is likely through increased microbial turnover, and sustained high-quality food for nematodes.

Introduction

Anthropogenic nitrogen (N) deposition has increased more than an order of magnitude over the last century and is far greater than N deposition from natural sources (Galloway et al. 2004, Galloway et al. 2008). Largely from food and energy manufacture and use, N deposition can have extensive effects on greenhouse gases, above- and belowground biodiversity, and soil biogeochemical cycles (Tilman 1986, Vitousek et al. 1997, Sala et al. 2000, Gough et al. 2012, Ramirez et al. 2012). These effects are not isolated to human-managed systems, and reach even very secluded places (Fenn et al. 2003, Pardo et al. 2011). While the impacts of N deposition aboveground generally include increased primary production, which stores carbon (Quinn et al. 2009), belowground responses differ by ecosystem (Liu and Greaver 2010, Lu et al. 2011, Zhou et al. 2014). These responses vary from soil net carbon storage (e.g. forests, Janssens et al. 2010) to net loss (e.g. arctic tundra, Mack et al. 2004).

A long-term nitrogen addition study in the subalpine forest of the Colorado Rocky Mountains found that soil organic horizon carbon decreased by 11% in fertilized plots compared to control plots (Boot et al. 2016), which contrasts findings in other forests undergoing N amendments (e.g. Frey et al. 2014). Additional results from this study included reduced soil pH and microbial biomass; these results are more typical of N addition studies (Boot et al. 2016). Reduced microbial biomass after N addition is often attributed to lower plant C flux through reduced litter, root growth, and exudate input (Liu and Greaver 2010), but could also be a result of increased aluminum toxicity caused by lower soil pH (Vitousek et al. 1997). Although food

web dynamics are often left out of N addition studies, elevated grazing by soil fauna resulting in increased turnover could explain the loss of microbial biomass (Lokupitiya et al. 2000, Parfitt et al. 2010).

Nematoda is an incredibly diverse phylum, ubiquitous in soil. Nematodes span multiple trophic groups, with different taxa feeding on fungi, bacteria, cyanobacteria, algae, protozoans, roots, and other soil fauna (Yeates et al. 1993, Wardle et al. 1995, Bongers and Bongers 1998). Because they occupy many trophic levels and are sensitive to environmental changes, their communities reveal the soil's condition and are useful as environmental and food web indicators (Bongers 1990, Ruess et al. 1999, Ferris et al. 2001, Yeates 2003). The successional maturity of nematode communities can be measured using the maturity index (MI; Bongers 1990). Briefly, undisturbed soil communities with sufficient resources have greater MI values than those from disturbed systems. The extensions of the MI – including the enrichment index (EI) and structural index (SI) – are useful for assessing soil food web structure and function (Ferris et al. 2001). Higher EI values indicate greater availability and turnover of resources, and are characterized by opportunistic groups; while greater SI values indicate low stress, high stability, and are generally systems where greater diversity, number of trophic links, and long-lived omnivore-predators are present (Ferris et al. 2001).

Commonly, opportunistic nematode groups (particularly r-selected bacterivores) increase in abundance with N-addition (Ettema et al. 1999, Lokupitiya et al. 2000, Ruess et al. 2002) while long-lived omnivore-predators decrease (Todd 1996, Sarathchandra et al. 2001), reflecting an increased abundance of resource availability along with stress caused by N addition. However, the effects of N addition on nematode community vary by ecosystem. For example, lower nematode abundance and diversity with N addition has been found in grasslands (Wei et

al. 2012) and temperate forests (Sun et al. 2013). Meanwhile, Zhao et al. (2014) showed that nematode diversity and trophic composition were unaffected by N addition for tropical forests. Nematodes likely track the ecosystem response to N addition rather than responding directly to elevated N.

The objective of our study was to use the MI and similar nematode community indices, to test the hypothesis that nematode community maturity and diversity are correlated negatively with long-term fertilization. We hypothesized a switch to a bacterial-driven, faster cycling soil food web with long-term nitrogen fertilization, which would be reflected by a lower MI, higher EI, lower SI, and overall significant increase in the total abundance of nematodes. We expected that nematode communities in control plots would have greater MI and SI, lower EI, greater richness and diversity values, and a distinct composition compared to fertilized plots.

Methods

Study site

Loch Vale watershed (LVWS) is located on the east side of the continental divide in Rocky Mountain National Park, Colorado, USA, where soils are shallow and coarse entisols (Baron et al. 1992). Located at about 3200m ASL in elevation, the mean annual temperature is 1.2 °C and mean annual precipitation is 105 cm (Mast et al. 2014). This area receives approximately 3 to 4 kg N ha^{-1} yr^{-1} as wet deposition (Baron et al. 2000). In 1996, a nitrogen fertilization experiment was established in LVWS in a split-plot design (for experiment details see: Rueth et al. 2003). Briefly, three pairs of experimental plots (30m x 30m) are located on undisturbed, closed-canopy, old growth Engelmann spruce and subalpine fir stands on northeast facing slopes. Each pair of plots includes one control and one fertilized plot. For fertilized plots,

dry ammonium nitrate (NH_4NO_3) was applied throughout the year to mimic natural atmospheric deposition. Specifically, NH_4NO_3 pellets were applied at a rate of 2.5 kg N ha^{-1} $month^{-1}$ from April to October and 7.5 kg N ha^{-1} after the first snow in October. In total 25 kg N^{-1} yr^{-1} was applied. The rate chosen was similar to natural atmospheric N deposition rates in other parts of the United States during the setup of the experiment in 1996.

Soil collection and analyses

In July 2014 and July 2015, 24 soil cores (5.5cm diameter x 10cm depth) were collected in the LVWS experimental plots (4 samples per each of 3 control and fertilized plots). Cores were taken approximately 3m apart in the innermost $15m^2$ area of experimental plots to minimize any edge effects. Samples were stored at 4° C at Colorado State University until processing. Soil nematodes were extracted within 48h of collection by the sugar centrifugation floatation method (Jenkins 1964; Freckman and Virginia 1993). Five nematode trophic groups (bacterivore, fungivore, plant parasite, omnivore, and predator) were identified according to Yeates et al. (1993) using an inverted microscope (Olympus CKX41, 200X magnification). After trophic group identification, 50 nematodes were randomly subsampled and identified to family level. Nematodes were assigned to colonizer–persister groups based on Bongers (1990). Additional fauna groups present in the soil extract were enumerated and included Rotifera, Tardigrada, and enchytraeids (Annelida). Mass loss of soils dried at 105° C for 48h was assessed to determine gravimetric soil moisture (water mass per unit soil mass). Soil fauna absolute abundance was then expressed on an oven dry weight basis as the number of individuals kg dry $soil^{-1}$. Bulk density was 37,004.73 ± 4632.92 g soil m^{-2} and 42986.22 ± 5013.79 g soil m^{-2} for control and fertilized plots, respectively (mean ± standard error).

Nematode community indices

We measured nematode family richness, family diversity, and ecological maturity indices of nematode communities (plant parasitic and free-living). Shannon diversity index was calculated to assess the diversity of families. Two nematode maturity indices were used: 1) the maturity index for free-living nematodes (MI) and 2) the plant-parasitic nematodes index (PPI). To calculate these indices, nematodes are first assigned a colonizer– persister value (*c–p*) ranging from enrichment colonizers (*c–p* = 1) and disturbance colonizers (*c–p* = 2) to persisters (*c–p* = 5). The MI is the weighted mean for the frequency distribution of collective *c–p* values. Specific details for MI and PPI calculations can be found in (Bongers 1990). Additionally, two maturity index extensions - the enrichment index (EI) and structural index (SI) – were calculated according to Ferris et al. (2001) to identify nematode food web properties.

Analysis of treatment effects

We assessed the effects of fertilization treatment and sampling year on nematode total absolute abundance, trophic group absolute abundance, family relative abundance, family diversity, and maturity indices with mixed effect models. Treatment and year were fixed effects and plot was random. We also tested these effects on rotifer, tardigrade and enchytraeid absolute abundances. We used Tukey's HSD for post-hoc comparisons. Distributions were assessed for normality and data were transformed (log x+1) when necessary to meet assumptions. For all analyses n=12. Statistical significance was accepted at alpha <0.05. All analyses were performed in R (Oksanen et al. 2013, R-Core-Team 2014)

Community ordinations

Non-metric multidimensional scaling (NMDS) was performed to show soil nematode community position in ordination space and to investigate if fertilization was a significant driver

of community structure. NMDS is a robust unconstrained ordination method often used for community ecology (Minchin 1987). Unlike other ordination techniques that rely on distances, such as Euclidean distances, NMDS relies on the rank order of dissimilarity in a community (Kruskal 1964). Using relative abundances of nematode families, we defined the original position of the community in multidimensional space using the bray-curtis distance coefficient. We then ran the NMDS with 1 through 6 dimensions and chose 6 dimensions as the best, rerunning the NMDS ordinations multiple times with several random starting configurations and then choosing the best configuration. This returned a stress value of 4.5%. Permutational multivariate analysis of variance (PERMANOVA) was used to test if communities significantly grouped by treatment. All of these analyses were performed in R using the vegan package (Oksanen et al. 2013, R-Core-Team 2014).

Results

Thirteen nematode families were identified in subalpine soils (Table 5.1). All families were found in both treatments, except Aporcelaimidae, which was only found in control plots. Treatment was a significant main effect on the relative abundance of all bacterivore families: Plectidae, Rhabditidae, Cephalobidae, plant parasitic Tylenchidae, fungivorous Aphelenchidae, and predaceous Aporcelaimidae. In fertilized plots, Rhabditidae and Tylenchidae made up a greater proportion of the community compared to control plots (Table 5.1, LSMeans, $p<0.05$), while Aphelenchidae, Aporcelaimidae, Cephalobidae, and Plectidae made up a greater proportion of the community in the control (Table 5.1).

Dissimilarity tests based on the Bray-Curtis distance showed that nematode communities from fertilized plots were significantly different from the control plots when assessed at the

family level (Fig. 5.1, PERMANOVA p=0.001). The community structure shifted significantly from 2014 to 2015 (Fig 5.1, PERMANOVA p=0.006) with a significant decrease in the relative abundance of Aphelenchidae and an increase in Dorylaimidae and Monochidae for control plots (Table 5.1).

Total nematode abundance, plant parasitic nematode abundance, EI, and PPI were significantly greater in fertilized plots (Table 5.2), while family richness, Shannon diversity, and MI were significantly greater in control plots (Table 5.2). The community structure (e.g. relative abundances) were more variable by year in the control plot (Table 1), while the absolute abundance was more variable by year in the fertilized plots despite relative abundances remaining constant (Table 5.2). We enumerated additional soil fauna – rotifers, tardigrades, and enchytraeids – that were present in the sample extracts, and rotifers were also significantly more abundant in the fertilized plots (Table 5.2).

We observed an inverse relationship between the nematode MI and the PPI (Fig 5.2), where the MI was significantly lower but the PPI was significantly greater in fertilized plots compared to control plots (Table 5.2). Additionally, EI values were significantly greater in fertilized plots while there was no significant difference in SI values between control and fertilized (Table 5.2 and Fig 5.3). On the structure-enrichment plot, both control and fertilized communities were structured and enriched (quadrat B, Fig 5.3).

Discussion

As hypothesized, the nematode community was more diverse and ecologically mature in control compared to fertilized plots. The relative dominance of rhabditid bacterivores and tylenchid plant parasites in fertilized plots was associated with lower ecological maturity. Both

are opportunistic and respond rapidly to flushes of resources. Lokupitiya et al. (2000) and Ruess et al. (2002) observed similar shifts in nematode community with N addition. For *c-p* 1 bacterivores to dominate 19 years after N addition began, suggests that the enrichment and turnover through the bacterial pathway is sustained over time. Bongers et al (1997) found similar results and showed that differences in nematode communities (as evidenced by MI) persisted for 19 years even after nutrient addition ceased.

We also observed a significant increase in the PPI in fertilized plots compared to control plots. An increase in the plant parasitic index is related positively to soil nutrient enrichment, and has been observed systems undergoing N amendments (Bongers et al. 1997). The MI and PPI are two indices that respond in opposite directions at increased nutrient availability (Bongers et al. 1997). The MI decreases as a result of an increasing proportion of enrichment opportunists, the PPI increases, we assume, by an increased carrying capacity for plant parasitic nematodes, and particularly for tylenchid plant parasites (Bongers et al. 1997), which are root associates (Yeates et al. 1993). However, some studies have found no changes in the PPI with nitrogen addition (Li et al. 2013, Song et al. 2016), and these results could be due to plant species identity (Wardle et al. 2003) and their differing responses to N addition.

We expected the fertilized nematode communities to have a higher EI and a lower SI than the control. The structure-enrichment plot (Fig 5.3) reflects an increase in trophic linkages along the x-axis (SI) and in reproductive potential along y-axis (EI). We expected control communities in the structure-enrichment plot to fall into quadrat C, which is typical for undisturbed forests (Ferris et al. 2001). Both control and fertilized plots fall into quadrat B (Fig 5.3), where fertilized communities have a significantly greater EI than control (Table 5.2). Communities in quadrat B are characterized as diverse, mature food webs, occur in ecosystems that are N-enriched, and

experience low levels of disturbance (Ferris et al. 2001). The high enrichment of the control communities may be due to the natural atmospheric N deposition, which is an order of magnitude greater than pre-European settlement background values (Baron 2006). Additionally, we expected that N addition would disturb the nematode communities and cause a loss of the omnivores and predators (*c-p* 4 and 5), but only the predator Aporcelaimidae was negatively affected by N addition (Table 5.1). Other groups such as Dorylaimidae and Monochidae were not affected by N addition and overall there was no difference in total Omnivore and Predator abundance between the treatments (Table 5.2). As a result, both fertilized and control plots were structured (no significant differences between SI, Table 5.2 and Fig 5.3), with equal trophic links.

Despite soil sampling on the same calendar date each year, the variation in nematode communities by year could be due to differences in season, such as total precipitation, timing of snowmelt, or soil moisture, which varies from year to year in the subalpine ecosystem. Total annual precipitation was greater in 2014 than 2015, (138 cm *vs* 117 cm, respectively; NADP). The nematode community reflected these temporal differences as evidenced by a lower relative abundance of omnivores and higher relative abundance of bacterivores in 2014 control plots. Other studies have shown that omnivore nematode populations (e.g. dorylaimids) decline during winter (Wasilewska 1971) and after high precipitation (Sun et al. 2016) while bacterivores increase during cold, wet periods (Sohlenius 1985).

In conclusion, we characterized the nematode communities in fertilized and control plots in a long-term N addition study in a subalpine forest. Nematode communities are distinct between treatments and are more diverse and successionally mature in control plots. Higher abundance of nematodes and an enriched food web characterized by opportunistic taxa was

sustained even 19 years after treatments began. Changes in nematode community have ecosystem implications. In a meta-analysis, Sackett et al. (2010), found that soil fauna had a positive effect on the growth of coniferous plants, suggesting increased abundance of soil fauna could impact the growth of coniferous forests. Further, our study complements findings of Boot et al. (2016) and suggests that lower microbial biomass in N-amended plots may be linked to top-down control by soil fauna.

Table 5.1: Nematode families shown by their trophic group, colonizer-persister value (*c-p*), and relative abundance by year and treatment (mean ± standard error, n=12). Significant results from the mixed model for each family are shown (p<0.05); T= treatment and Y=year. Different lowercase letters denote significant differences across treatments and years (LSMeans, p<0.05). Groups with no letters had no significant differences between years/treatments.

Trophic group	*c-p*	Family	Control		Fertilized		Model Summary
			2014 (%)	2015 (%)	2014 (%)	2015 (%)	
Bacterivore	2	Plectidae	0.08±0.01**a**	0.04±0.01**a**	0.04±0.01**bc**	0.05±0.01**ac**	T, Y, T*Y
	1	Rhabditidae	0.07±0.01**a**	0.06±0.01**a**	0.22±0.04**b**	0.25±0.04**b**	T
	2	Cephalobidae	0.10±0.02**a**	0.11±0.01**a**	0.03±0.01**b**	0.06±0.01**b**	T
Fungivore	2	Aphelenchidae	0.10±0.02**a**	0.02±0.00**b**	0.01±0.00**b**	0.01±0.01**b**	T
	2	Aphelenchoididae	0.28±0.02**ab**	0.29±0.02**ab**	0.31±0.03**a**	0.20±0.02**b**	T*Y
Plant parasite	2	Tylenchidae	0.03±0.01**a**	0.06±0.01**a**	0.15±0.02**b**	0.12±0.02**b**	T
	3	Hoplolaimidae	0.02±0.00	0.01±0.00	0.02±0.00	0.04±0.01	
	3	Dolichodoridae	0.04±0.01	0.01±0.00	0.02±0.00	0.05±0.02	T*Y
	3	Criconematidae	0.03±0.02	0.02±0.00	0.02±0.01	0.01±0.00	
	3	Pratylenchidae	0.01±0.00	0.01±0.00	0.01±0.00	0.01±0.00	
Predator & Omnivore	4	Dorylaimidae	0.08±0.01**a**	0.16±0.02**b**	0.09±0.02**a**	0.08±0.02**a**	Y, T*Y
	5	Aporcelaimidae	0.07±0.02**a**	0.04±0.01**a**	0.00±0.00**b**	0.00±0.00**b**	T
	4	Monochidae	0.05±0.01**a**	0.12±0.02**bc**	0.03±0.01**a**	0.08±0.02**ac**	Y

Table 5.2. Mean values of nematode diversity, nematode community indices, nematode trophic group abundances, and other soil fauna groups (±standard error, n=12). Significant results from the mixed model are shown (p<0.05). Different letters denote significant differences across treatments and years (LSMeans, p<0.05). Groups with no letters had no significant differences between years/treatments.

	Control		Fertilized		Model
	2014	2015	2014	2015	Summary
Nematode abundance (kg soil^{-1})	20484±3343**ac**	11356±2108**b**	40168±9227**a**	15854±1458**bc**	T, Y
Nematode family richness	10.67±0.38**a**	9.67±0.48**ac**	8.17±0.55**b**	8.33±0.45**bc**	T
Shannon diversity (H')	2.04±0.04**a**	1.90±0.05**ac**	1.64±0.06**b**	1.82±0.07**bc**	T, T*Y
Nematode trophic group abundance (kg soil^{-1})					
Bacterivore	7245±1123**a**	2366±385**b**	12507±3179**a**	5436±317**a**	Y, T*Y
Fungivore	6154±1244**abc**	3096±550**ac**	13318±4368**b**	3541±746**c**	Y
Plant parasite	2440±407**ab**	1628±430**a**	8194±2232**b**	3838±560**b**	T
Omnivore	3030±655**a**	2423±712**ab**	4073±1474**a**	1116±199**b**	
Predator	932±217	1288±305	876±180	1405±294	
Nematode community indices					
MI	2.05±0.10**a**	2.28±0.08**a**	1.46±0.08**b**	1.52±0.11**b**	T
PPI	0.35±0.06**ac**	0.25±0.04**ab**	0.47±0.07**bd**	0.54±0.09**cd**	T
EI	53.61±1.80**a**	54.17±1.96**a**	74.55±3.07**b**	77.25±3.71**b**	T
SI	60.99±3.36**ab**	73.00±2.94**ac**	50.85±7.34**b**	64.02±4.50**bc**	
Other soil fauna abundances (kg soil^{-1})					
Rotifers	960±227**a**	1373±242**ab**	2297±449**b**	1627±398**ab**	T
Tardigrades	763±254	442±81	976±409	864±214	
Enchytraeids	114±30	217±57	187±62	133±31	

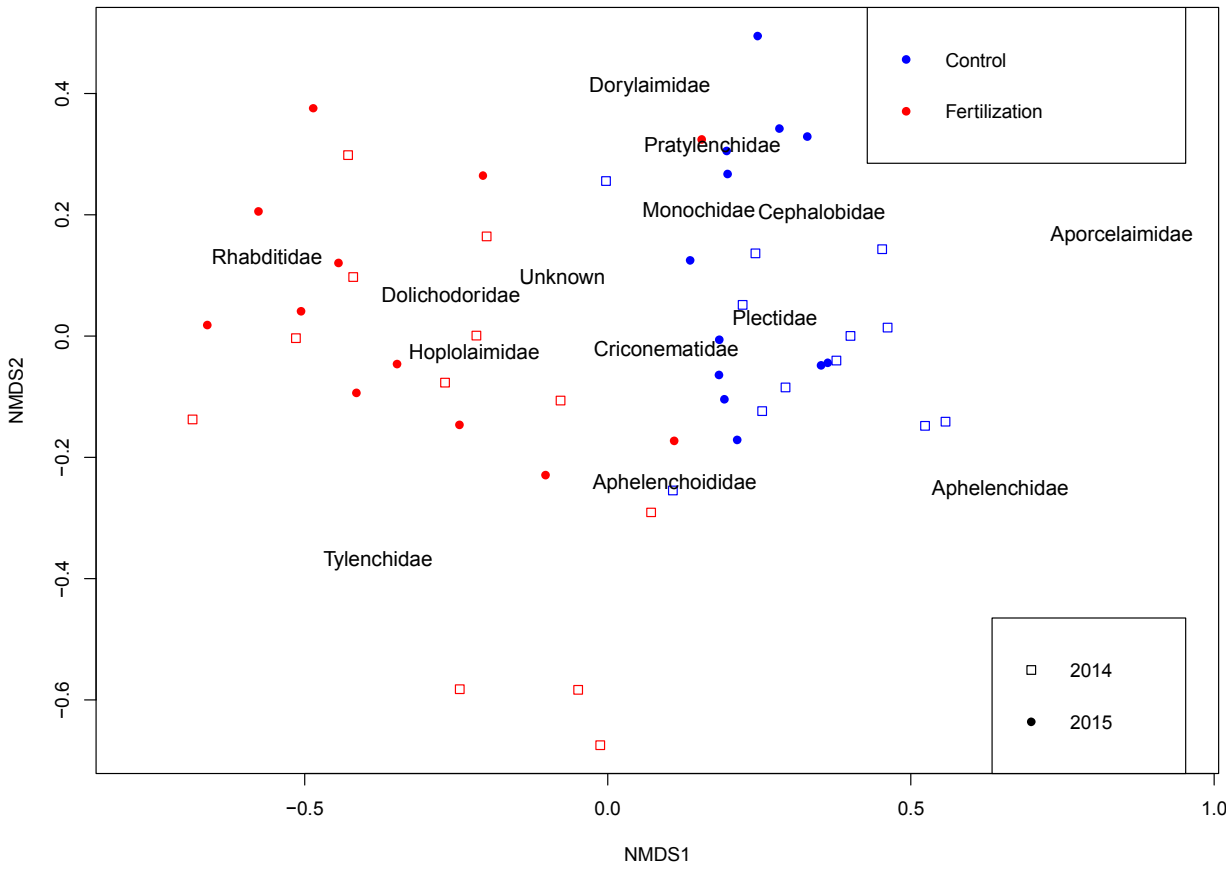


Figure 5.1: NMDS ordination (Bray-Curtis dissimilarity) of nematode communities based on relative abundances of nematode families. Each point reflects the community found in an individual sample (n=12 per treatment x 2 years). Points that are close together have more similar communities than points that are far apart. Colors show treatment: fertilized is red and control is blue. Shapes show year: open squares are 2014 and filled circles are 2015. Names of families are overlaid.

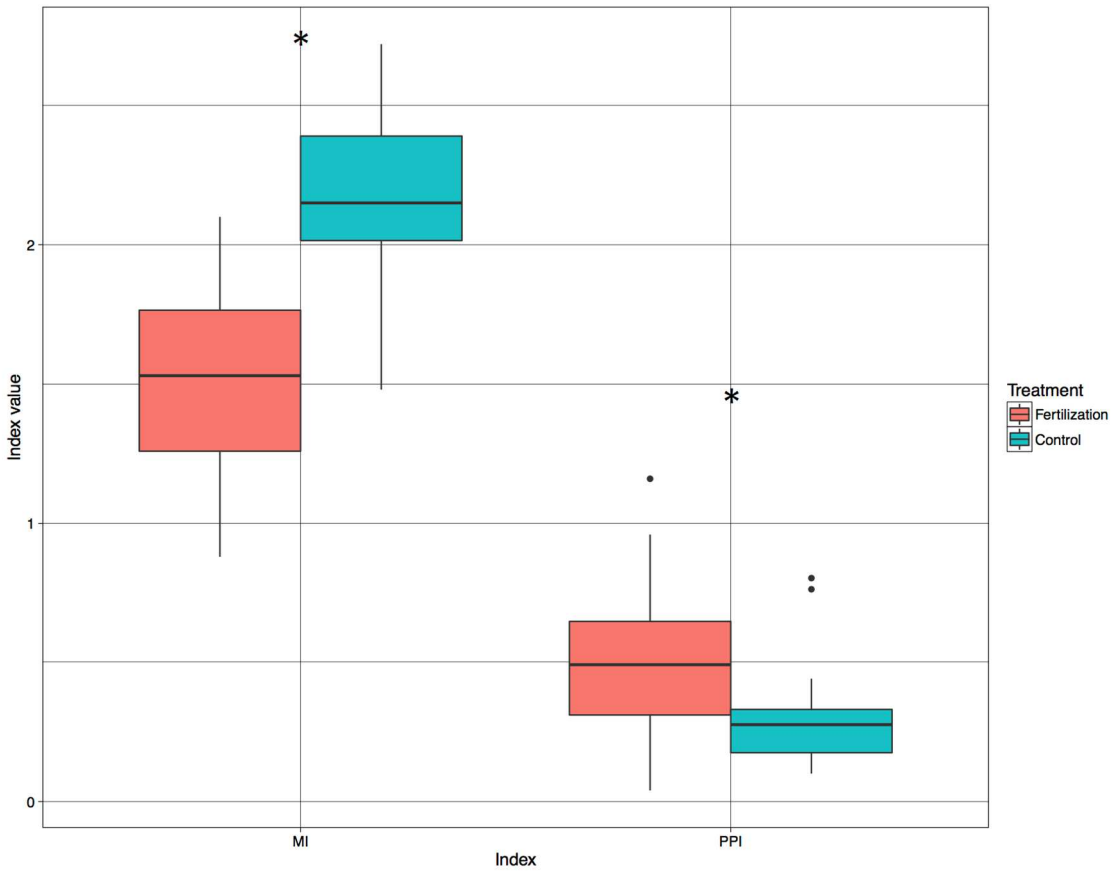


Figure 5.2: Maturity index and plant parasite index. Colors show treatment: fertilized is red and control is blue. Asterisks denote significant differences in treatment effects ($p<0.05$).

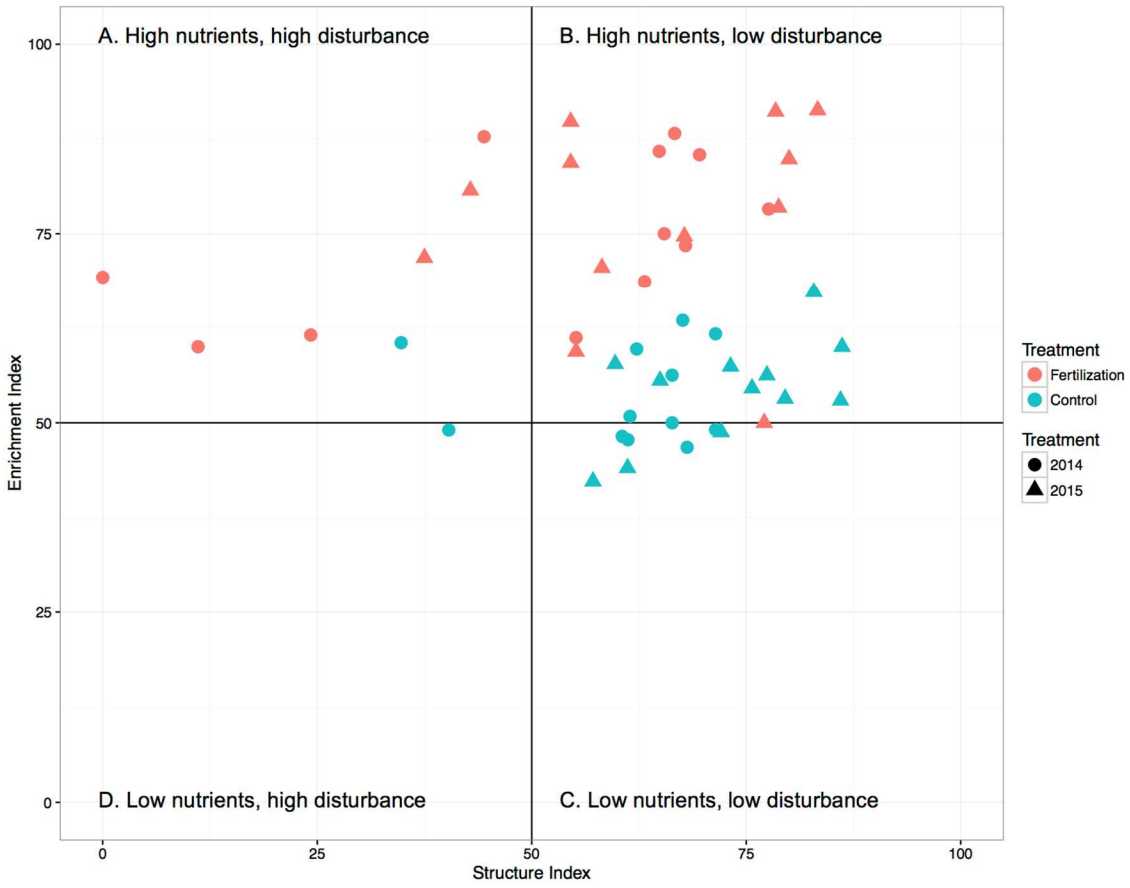


Figure 5.3: Structure-Enrichment plot. Quadrats are labeled A thru D after Ferris et al. (2001). Colors show treatment: fertilized is red and control is blue. Shapes show year: circles are 2014 and triangles are 2015.

CHAPTER 6 – CONCLUSIONS

This dissertation advances our understanding of trophic structure and biological interactions in soil food webs. By defining Antarctic soil food web structures at various scales using stable isotopes (Figs 6.1 and 6.2), implementing a laboratory microcosm experiment with soil collected in the McMurdo Dry Valleys, and analyzing soil nematode food web indices for a long-term nitrogen addition study in the subalpine ecosystem in Colorado, I answered four questions (see Chapter 1) designed to increase the knowledge of the soil food web and how its biotic interactions structure soil communities. Using stable isotope analysis (^{13}C and ^{15}N) of soil fauna presented in Chapter 2, we found that the nematode *Eudorylaimus antarcticus* occupies the omnivore-predator trophic position in the McMurdo Dry Valleys wet soil food web, which is consistent with previous predictions (Freckman and Virginia 1997) and matches the trophic level of this genus from differing ecosystems (McSorley 2012). By defining the soil food web structure for the wet soil habitat in the McMurdo Dry Valleys (Fig 6.1), this chapter shows that biological interactions (e.g. predator-prey) at least exist in this ecosystem and this set the stage for further tests of biological interactions' role in community structure in this system.

In Chapter 3, we experimentally tested the role of biological interactions in structuring soil communities in McMurdo Dry Valley soils under differing environmental treatments (salinity and moisture). Prior predictions suggest that biological interactions do not play a role in structuring Antarctic soil communities (Hogg et al. 2006), especially since biological interactions have long been accepted as weakest at high latitudes (Schemske et al. 2009). However, there is not much empirical support for greater biological interactions (e.g. mutualisms, host-parasite, and predator-prey) at low latitudes (Ollerton 2012). Furthermore, our experiment results

indicated that *Scottnema lindsayae* has top down control on bacteria populations, which is alleviated under high stress (salinity), showing that biological interactions play a role in community structure in soils from as far as 77°S. Additionally, these results suggest that saline soil could be a potential escape from predation for bacteria. This is an interesting result given that increasing hydrological connectivity in the McMurdo Dry Valleys is expected to redistribute salts and solutes across the landscape, altering soil habitats (Gooseff et al. 2017b).

In Chapter 4, we tested soil food web structure in McMurdo Dry Valley soils as was done in Chapter 1, but we expanded this to 8 valleys (from coastal to high elevation) and multiple habitat types (wet and dry) across the valleys to test if habitat and productivity (assumed to be lower with greater distance to coast and higher elevation) affected soil food web structure. Our results showed that soil food webs vary across the landscape and that wet soil food web structure is consistent with results of Chapter 1 (Fig 6.1). However, dry soil food webs were simpler than wet food webs. Generally, dry food webs had either one or two invertebrate consumers present (Fig 6.2): *S. lindsayae* and *E. antarcticus*. Surprisingly, *E. antarcticus* was a primary consumer in dry habitat (supported by isotopic evidence), which is likely due to a switch from predator to consumer when resource availability is low (Diehl and Feissel 2001). Additionally*, S. lindsayae* from the oldest soils (dry habitat) had very light $\delta^{13}C$ signatures, indicating very old and highly processed C sources. However, *S. lindsayae* from these same age soils that were in wet habitat had $\delta^{13}C$ signatures that reflected recent C inputs into the system. These results echo those from Chapter 2, and indicate that increased hydrological connectivity in the dry valleys could alter soil resources, which feeds back into the trophic structure of soil food webs.

In Chapter 5, we examined whether biological interactions structure communities in the more diverse subalpine forest ecosystems in Colorado. Sampling soil from a long-term N

addition study, we found that nematode abundance was greater under N fertilization and that communities were shifted to a faster-cycling, bacterial driven system (as evidenced by a lower maturity index in the fertilized plots; e.g. Bongers 1990). Functional grouping of nematodes and maturity indices of nematode families showed a shift in the nematode community towards *r*-selected bacterivores for fertilized plots. Sustained top down effects of bacterivore nematodes on bacteria may explain lower microbial biomass and soil organic C in the same plots (Boot et al. 2016). These results indicate that top down effects of nematodes on bacteria extend beyond Antarctic soils (e.g. Chapter 2) and feedback to ecosystem functions such as carbon storage.

Currently, all biodiversity is undergoing a 6th great extinction, exacerbated by climate change. While there is a global effort to understand biodiversity, its drivers, and its changes (e.g. McGill et al. 2015), little is known about the immense biodiversity in soils (Phillips et al. 2017), or the complicated biological relationships that are hidden there (Wolkovich 2016). This dissertation contributes significantly to our understanding of soil food web structure and function in the McMurdo Dry Valleys, but it is also evident that significant gaps remain. For example, protists are widespread throughout the dry valleys (Bamforth et al. 2005), but were not considered in our work due to difficulty isolating taxa and quantifying isotopic signatures. These are likely important players in this system and should be considered explicitly in future studies. We found evidence for microbivore nematode control on bacteria populations in both Antarctic and subalpine soil ecosystems, but we did not quantify consumption or estimate turnover in these systems. Isotopic labeling studies could be used to better understand the feedback of these biological interactions to ecosystem functions. Furthermore, we found that soil food web structure varies across the landscape with habitat, but we did not specifically quantify soil organic carbon compounds or microbial communities at each sample location. Additional studies

that match soil invertebrate food webs to their specific resources would better inform spatial predictions of soil food webs and their expected shifts under climate change. Overall, the results of this dissertation represent significant improvements to the understanding of soil communities and their food web structure in Antarctica (Fig 6.1 and 6.2) and contribute to improved theory on the role of biological interactions in soil communities.

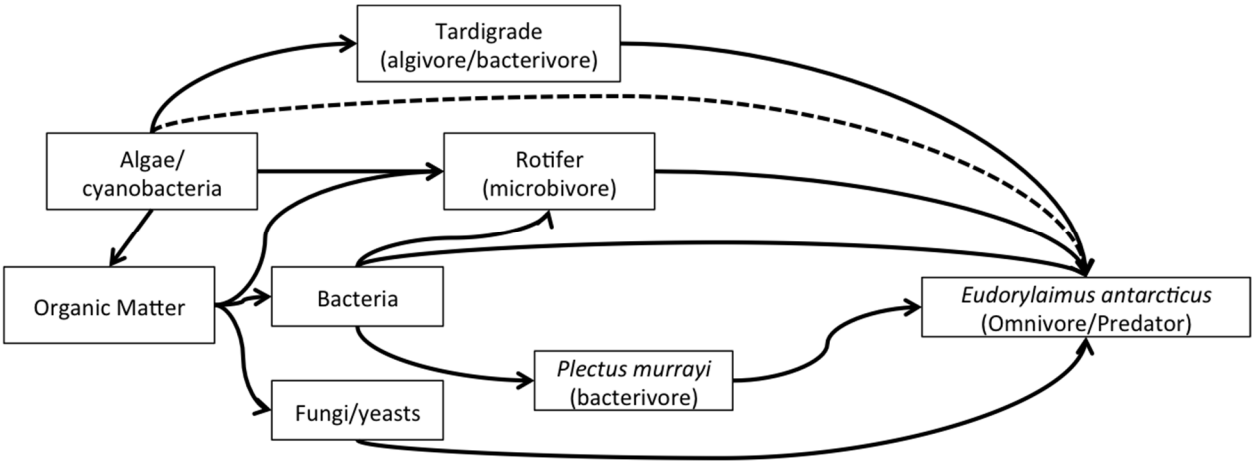


Figure 6.1. McMurdo Dry Valley wet soil food web diagram showing realized relationships (solid lines) based on isotopic evidence and potential relationships (dashed lines) based on evidence from other habitats or studies (Wall 2007)

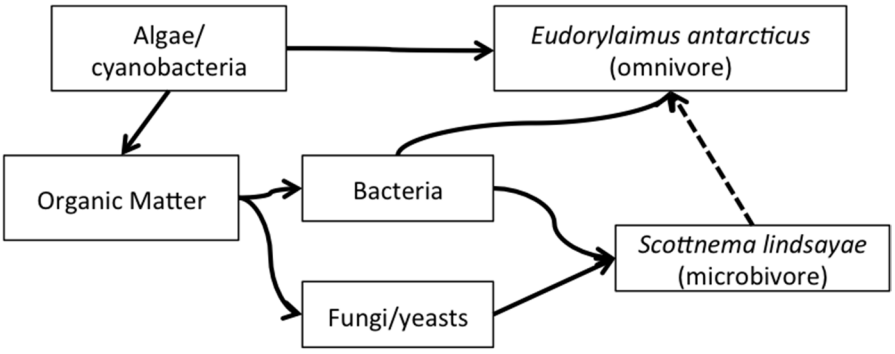


Figure 6.2. McMurdo Dry Valley dry soil food web diagram showing realized relationships (solid lines) based on isotopic evidence and potential relationships (dashed lines) based on evidence from other habitats

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APPENDIX 1 – SAMPLE COLLECTION DETAILS

Table A.1.1 Record of samples collected by valley and year

Location	Habitat	Elevation	latitude	longitude	Date sampled
Bonney	Dry	High	-77.6585	162.7519	13-Jan-17
Bonney	Dry	High	-77.6587	162.7541	13-Jan-17
Bonney	Wet	High	-77.6591	162.7673	13-Jan-17
Bonney	Wet	High	-77.6591	162.7673	13-Jan-17
Bonney	Dry	High	-77.6578	162.9173	13-Jan-15
Bonney	Dry	High	-77.6586	162.9199	13-Jan-15
Hoare	Dry	High	-77.6378	162.8874	19-Jan-15
Hoare	Dry	High	-77.6378	162.8873	19-Jan-15
Beacon	Dry	NA	-77.8234	160.6202	18-Jan-17
Beacon	Dry	NA	-77.8235	160.6200	18-Jan-17
Beacon	Dry	NA	-77.8234	160.6202	18-Jan-17
Beacon	Dry	NA	-77.8232	160.6200	18-Jan-17
Beacon	Dry	NA	-77.8233	160.6206	18-Jan-17
Beacon	Dry	NA	-77.8233	160.6177	18-Jan-17
Beacon	Dry	NA	-77.8231	160.6158	18-Jan-17
Beacon	Dry	NA	-77.8230	160.6155	18-Jan-17
Beacon	Dry	NA	-77.8232	160.6154	18-Jan-17
Beacon	Dry	NA	-77.8232	160.6154	18-Jan-17
Beacon	Dry	NA	-77.8233	160.6180	18-Jan-17
Beacon	Dry	NA	-77.8234	160.6200	18-Jan-17
Beacon	Dry	NA	-77.8234	160.6198	18-Jan-17
Beacon	Dry	NA	-77.8214	160.6213	22-Jan-16
Beacon	Dry	NA	-77.8214	160.6213	22-Jan-16
Beacon	Dry	NA	-77.8214	160.6213	22-Jan-16
Beacon	Dry	NA	-77.8214	160.6213	22-Jan-16
Bonney	Dry	Low	-77.7245	162.3141	12-Jan-17
Bonney	Wet	Low	-77.7247	162.3148	12-Jan-17
Bonney	Dry	NA	-77.7273	162.3241	17-Jan-15
Bonney	Wet	NA	-77.7283	162.3239	17-Jan-15
Bonney	Dry	NA	-77.7247	162.3116	17-Jan-15
Bonney	Wet	NA	-77.7247	162.3117	17-Jan-15
Garwood	Dry	NA	-78.0177	163.8794	6-Jan-17
Garwood	Dry	NA	-78.0177	163.8794	6-Jan-17
Garwood	Wet	NA	-78.0177	163.8794	6-Jan-17
Garwood	Wet	NA	-78.0177	163.8794	6-Jan-17
Garwood	Wet	NA	-78.0177	163.8794	6-Jan-17
Garwood	Wet	NA	-78.0177	163.8794	6-Jan-17

Garwood	Dry	NA	-77.0211	163.8993	6-Jan-17
Garwood	Dry	NA	-77.0211	163.8993	6-Jan-17
Garwood	Wet	NA	-77.0211	163.8993	6-Jan-17
Garwood	Wet	NA	-77.0211	163.8993	6-Jan-17
Garwood	Wet	NA	-77.0211	163.8993	6-Jan-17
Garwood	Wet	NA	-77.0211	163.8993	6-Jan-17
Garwood	Dry	NA	-78.0367	164.0794	21-Jan-15
Garwood	Wet	NA	-78.0378	164.0669	21-Jan-15
Garwood	Dry	NA	-78.0897	164.1319	21-Jan-15
Garwood	Wet	NA	-78.0919	164.1350	21-Jan-15
Hjorth	Wet	Low	-77.5382	163.5669	10-Jan-17
Hjorth	Wet	Low	-77.5382	163.5674	10-Jan-17
Hjorth	Wet	Low	-77.5386	163.5627	10-Jan-17
Hjorth	Wet	Low	-77.5384	163.5614	10-Jan-17
Upland Ponds	Dry	High	-77.7011	162.7063	21-Jan-16
Upland Ponds	Dry	High	-77.7008	162.7064	21-Jan-16
Upland Ponds	Dry	High	-77.7002	162.7148	21-Jan-16
Upland Ponds	Dry	High	-77.7015	162.7148	21-Jan-16
Upland Ponds	Wet	High	-77.7010	162.7090	21-Jan-16
Upland Ponds	Wet	High	-77.7011	162.7092	21-Jan-16
Upland Ponds	Wet	High	-77.7005	162.7120	21-Jan-16
Upland Ponds	Wet	High	-77.7006	162.7124	21-Jan-16
Miers	Wet	NA	-78.0887	163.7729	6-Jan-17
Miers	Wet	NA	-78.0887	163.7558	6-Jan-17
Miers	Wet	NA	-78.0888	163.7727	6-Jan-17
Miers	Wet	NA	-78.0888	163.7738	6-Jan-17
Miers	Wet	NA	-78.0946	163.7990	6-Jan-17
Miers	Wet	NA	-78.0946	163.7996	6-Jan-17
Miers	Wet	NA	-78.0948	163.7998	6-Jan-17
Miers	Wet	NA	-78.0945	163.7985	6-Jan-17
Miers	Dry	NA	-78.0890	163.7734	20-Jan-15
Miers	Wet	NA	-78.0890	163.7733	20-Jan-15
Miers	Dry	NA	-78.0941	162.7882	20-Jan-15
Miers	Wet	NA	-78.0942	163.7884	20-Jan-15
Hoare	Dry	High	-77.6221	162.9062	13-Jan-17
Hoare	Wet	High	-77.6221	162.9062	13-Jan-17
Upland Ponds	Wet	High	-77.6542	162.9135	21-Jan-16
Upland Ponds	Wet	High	-77.6544	162.9133	21-Jan-16
Upland Ponds	Wet	High	-77.6533	162.9181	21-Jan-16
Upland Ponds	Wet	High	-77.6533	162.9181	21-Jan-16
Upland Ponds	Dry	High	-77.6541	162.9095	21-Jan-16
Upland Ponds	Dry	High	-77.6542	162.9098	21-Jan-16
Upland Ponds	Dry	High	-77.6529	162.9095	21-Jan-16

Upland Ponds	Dry	High	-77.6530	162.9209	21-Jan-16
Fryxell	Dry	High	-77.6284	163.3778	11-Jan-15
Fryxell	Dry	High	-77.6291	163.3723	11-Jan-15
Fryxell	Dry	High	-77.6266	163.3561	11-Jan-15
Fryxell	Dry	High	-77.6254	163.3618	11-Jan-15
Garwood	Dry	NA	-78.0344	164.1442	21-Jan-15
Garwood	Dry	NA	-78.0341	164.1403	21-Jan-15
Garwood	Wet	NA	-78.0336	164.1363	21-Jan-15
Garwood	Dry	NA	-78.0290	164.1468	21-Jan-15
Garwood	Dry	NA	-78.0286	164.1484	21-Jan-15
Garwood	Dry	NA	-78.0284	164.1504	21-Jan-15
Fryxell	Dry	High	-77.6139	163.3109	10-Jan-15
Fryxell	Dry	High	-77.6139	163.3153	10-Jan-15
Fryxell	Dry	High	-77.6123	163.3233	10-Jan-15
Fryxell	Dry	Low	-77.6080	163.2540	20-Jan-14
Fryxell	Dry	Low	-77.6080	163.2542	20-Jan-14
Fryxell	Dry	Low	-77.6080	163.2544	20-Jan-14
Fryxell	Wet	Low	-77.6080	163.2533	20-Jan-14
Fryxell	Wet	Low	-77.6080	163.2535	20-Jan-14
Fryxell	Wet	Low	-77.6081	163.2539	20-Jan-14
Hoare	Dry	High	-77.6373	162.8865	18-Jan-17
Hoare	Dry	High	-77.6374	162.8868	18-Jan-17
Hoare	Low	Dry	-77.6331	162.8825	18-Jan-17
Hoare	Low	Dry	-77.6331	162.9827	18-Jan-17
University	Dry	NA	-77.8622	160.7111	18-Jan-17
University	Dry	NA	-77.8631	160.7002	18-Jan-17
University	Dry	NA	-77.8631	160.6995	18-Jan-17
University	Dry	NA	-77.8632	160.6981	18-Jan-17
University	Dry	NA	-77.8626	160.7041	18-Jan-17
University	Dry	NA	-77.8626	160.7048	18-Jan-17
University	Dry	NA	-77.8621	160.7087	18-Jan-17
University	Dry	NA	-77.8617	160.7126	18-Jan-17
University	Dry	NA	-77.8617	160.7125	18-Jan-17
University	Dry	NA	-77.8615	160.7128	18-Jan-17
University	Dry	NA	-77.8615	160.7128	18-Jan-17
Virginia	Dry	NA	-77.4919	160.9307	23-Jan-17
Virginia	Dry	NA	-77.4919	160.9309	23-Jan-17
Virginia	Dry	NA	-77.4919	160.9307	23-Jan-17
Virginia	Dry	NA	-77.4903	160.9340	23-Jan-17
Virginia	Dry	NA	-77.4903	160.9339	23-Jan-17
Virginia	Dry	NA	-77.4902	160.9340	23-Jan-17
Virginia	Dry	NA	-77.4911	160.9349	23-Jan-17
Virginia	Dry	NA	-77.4910	160.9346	23-Jan-17

Wall	Dry	NA	-77.4957	160.8459	23-Jan-17
Wall	Dry	NA	-77.4958	160.8448	23-Jan-17
Wall	Dry	NA	-77.4958	160.8443	23-Jan-17
Wall	Dry	NA	-77.4933	160.8527	23-Jan-17
Wall	Dry	NA	-77.4935	160.8529	23-Jan-17
Wall	Dry	NA	-77.4934	160.8531	23-Jan-17
Wall	Dry	NA	-77.4950	160.8527	23-Jan-17
Wall	Dry	NA	-77.4949	160.8543	23-Jan-17
Wright Brownworth	Wet	NA	-77.4321	162.7146	23-Jan-17
Wright Vanda	Dry	NA	-77.5187	161.6932	23-Jan-17
Wright Dias	Dry	NA	-77.5411	161.0720	23-Jan-17
Wright Brownworth	Wet	NA	-77.4320	162.7144	23-Jan-17
Wright Vanda	Dry	NA	-77.5188	161.6933	23-Jan-17
Wright Dias	Dry	NA	-77.5412	161.0723	23-Jan-17
Wright Brownworth	Wet	NA	-77.4320	162.7136	23-Jan-17
Wright Vanda	Dry	NA	-77.5188	161.6933	23-Jan-17
Wright Dias	Dry	NA	-77.5411	161.0722	23-Jan-17
Wright Brownworth	Wet	NA	-77.4323	162.7130	23-Jan-17
Wright Vanda	Dry	NA	-77.5190	161.6923	23-Jan-17
Wright Dias	Dry	NA	-77.5409	161.0702	23-Jan-17
Wright Brownworth	Wet	NA	-77.4324	162.7127	23-Jan-17
Wright Vanda	Dry	NA	-77.5189	161.6919	23-Jan-17
Wright Dias	Dry	NA	-77.5408	161.0707	23-Jan-17
Wright Brownworth	Wet	NA	-77.4328	162.7155	23-Jan-17
Wright Vanda	Dry	NA	-77.5185	161.6915	23-Jan-17
Wright Dias	Dry	NA	-77.5412	161.0708	23-Jan-17
Wright Brownworth	Wet	NA	-77.4327	162.7152	23-Jan-17
Wright Vanda	Dry	NA	-77.5185	161.6917	23-Jan-17
Wright Dias	Dry	NA	-77.5412	161.0707	23-Jan-17
Wright Brownworth	Wet	NA	-77.4326	162.7148	23-Jan-17
Wright Vanda	Dry	NA	-77.5185	161.6916	23-Jan-17
Wright Dias	Dry	NA	-77.5413	161.0706	23-Jan-17

APPENDIX 2 – SUPPLEMENTARY STUDY: SOIL FOOD WEBS IN CARBON-LIMITED SOIL RAPIDLY RESPOND TO ELEVATED CARBON IN A FIELD MICROCOSM EXPERIMENT

With low contemporary primary production, the McMurdo Dry Valley soils are extremely C limited and have soil organic carbon concentrations of 15 to 35μmol g^{-1} soil (Burkins et al. 2001). We asked: Will elevated C affect the dry soil food webs? We hypothesized that soil food webs would incorporate an influx of C, but this would take several active seasons to reach detectable levels in microbivores due to low temperatures that limit feeding, metabolism, and growth.

To test our hypothesis we established a field-based microcosm experiment to trace the flow of increased C through the soil food web near Many Glaciers Pond in Taylor Valley, Antarctica. Briefly, 19.6mg of ^{13}C-enriched mannitol (99.9 atom %) was added to 50g of fresh, unsterilized soil for each of 24 microcosms. In November 2014, microcosms in 50mL falcon tubes were established in the field. They were buried up to the top of the cap and caps were loosely covered with surrounding soil. Microcosms were collected at the end of January 2015 after one austral summer. Soil fauna were extracted from soil, identified under microscope, and collected for isotopic analysis of whole body biomass. Results showed the metazoan community consisted of one nematode species, *Scottnema lindsayae.* Population density of *S. lindsayae* was 1003±274 individuals kg^{-1} dry soil, comparable to nearby field data. Two months after C addition, *S. lindsayae* had incorporated mannitol-C in significant amounts. Nematode biomass from all samples was significantly enriched in ^{13}C vs. control samples. Overall, $\delta^{13}C$ was 21,760.07±3488.52‰ (Fig A2.1) and total nematode-C was 15.07 to 24.08% (95% CI) mannitol-derived. Total nematode C assimilation was 40-60 μg C kg soil. Rates of *S. lindsayae*

C-assimilation were comparable to previous findings in the dry valleys and on the same order of magnitude as nematodes of diverse temperate ecosystems (Barrett et al. 2008). This research reveals that Dry Valley food webs can rapidly respond to increased available C and incorporate this significantly into higher trophic level biomass. Our results have implications for Dry Valley C cycling under increased connectivity, and support the conclusion that modest changes in soil C can impact soil communities.

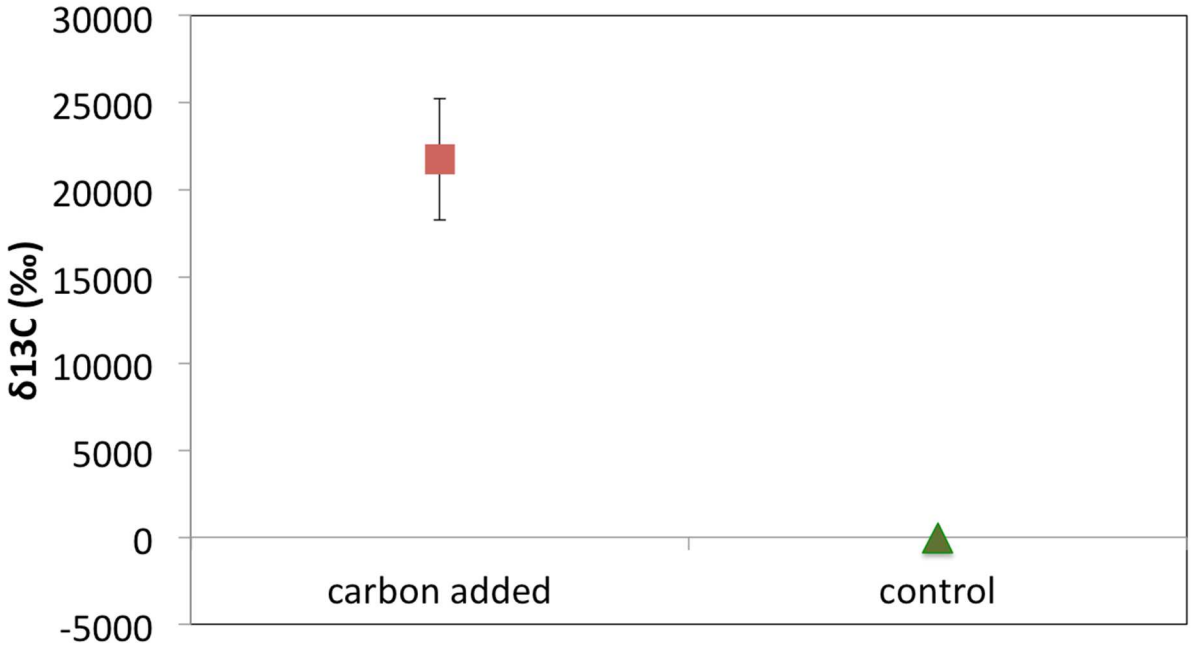

Figure A2.1: $\delta^{13}C$ values for *S. lindsayae* two months post C addition were 21760.07 ± 3488.52 and -26.31 ± 1.43 ‰ for C addition treatment and control, respectively (n=10)