

DISSERTATION

THE INFLUENCE OF MOISTURE AVAILABILITY ON TERRESTRIAL ECOSYSTEMS:  
EFFECTS ON SOIL ANIMAL COMMUNITIES ALONG A REGIONAL/GLOBAL SCALE  
CLIMATE GRADIENT

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## ABSTRACT

### THE INFLUENCE OF MOISTURE AVAILABILITY ON TERRESTRIAL ECOSYSTEMS: EFFECTS ON SOIL ANIMAL COMMUNITIES ALONG A REGIONAL/GLOBAL SCALE CLIMATE GRADIENT

Earth's climate is being altered at an alarming rate, and the consequences of these changes on the planet's ecosystems are unclear. In addition to increased warming due to rising CO<sub>2</sub> concentrations, alterations to precipitation patterns will influence soil moisture availability in terrestrial ecosystems and this will have important consequences for plant growth and the ability of soil systems to perform functions such as decomposition and nutrient cycling. The effects on soil systems are especially poorly understood, partly due to the many interactions between environmental conditions and the numerous species found within soil ecosystems, ranging from microbial organisms such as bacteria, archaea and fungi to soil animals including mites and nematodes.

With chapter 2, I provide an overview of the role of soil biodiversity and the implications climate and land-use changes may have for ecosystems as a consequence of their effects on soil biodiversity. I then examine the current state of understanding for the influence of soil moisture availability on plant and soil communities of temperate ecosystems in chapter 3, and highlight challenges for future research such as the inclusion of diversity metrics and soil animal community responses in climate change experiments as well as studies that operate at scales larger than single sites in order to better capture the dynamics of ecosystem changes.

My research focused on one aspect of climate change, the alteration of soil moisture availability within ecosystems due to changes in precipitation regimes, and whether it affected

soil organisms, particularly soil mites and nematodes (Chapter 4 of this dissertation). These two groups were selected because of their high abundances and diversity within soil ecosystems, their dependence upon soil water availability as a consequence of life history traits and their contributions to decomposition and nutrient cycling processes. To examine the effects of changing moisture availability on communities of mites and nematodes I analyzed soil samples along a large scale regional/global climate gradient made up of four long-term ecological research (LTER) sites including Konza Prairie LTER (KNZ), Kansas, Shortgrass Steppe LTER (SGS), Colorado, Jornada Basin LTER (JRN), New Mexico and McMurdo Dry Valleys LTER (MCM), Antarctica. I established elevation transects across hill slopes to obtain landscape-scale gradients of soil moisture availability within each of these ecosystems and sampled existing experimental manipulations of moisture availability from 2009-2011. Mites and nematodes were sorted to trophic groups to determine their ecological role and how changes to their abundances may affect ecosystems.

Mite and nematode abundances responded strongly to changes in moisture availability. Across the large-scale climate gradient of all four sites, a positive non-linear response was found with particularly large increases in animal abundances corresponding to incremental moisture increases at the lower limits of moisture availability. Within each of the ecosystems, however, the responses of soil animal trophic group abundances to moisture availability were very similar and were largely negative.

In chapter 5 of this dissertation, I further explore the effects of soil moisture and top-down or bottom-up community dynamics on mite and nematode abundances. To do this, I constructed a structural equation model examining the direct and indirect effects of soil moisture availability and trophic interactions on soil animal trophic group abundances. Results of this

model suggest that soil moisture strongly controls populations of these organisms. Additionally, predatory mite and nematode trophic groups have top-down controls on lower trophic groups, although these interactions do not appear to be due to predation and instead suggest the influence of additional, unmeasured environmental factors acting indirectly on lower-level soil animal trophic groups.

With this dissertation, I demonstrate that changes to soil moisture regimes can have important effects on soil animal communities. A review of the literature (Chapter 3 of this dissertation) showed altered soil moisture availability had the clearest effects on plants, with effects on soil organisms being more idiosyncratic, likely as a result of stronger indirect than direct effects. Experimental evidence along a regional/global climate gradient of two desert and two grassland sites (Chapter 4 of this dissertation) show that increases to moisture availability have strong positive effects on mite and nematode communities, especially at low levels of moisture availability across this large, multi-site scale. At smaller scales (within individual ecosystems) this response becomes weaker and results in declines to animal groups at most sites. These results suggest that as precipitation regimes are altered as a consequence of climate change, the resultant alterations to soil moisture availability may have important feedbacks to terrestrial ecosystems. Observed changes to trophic group structuring in response to changes in moisture availability (Chapters 4 and 5 of this dissertation) show that food webs may be restructured due to future changes in moisture availability, leading to increases to root herbivory and increasing the amount of energy flowing through bacterial rather than fungal decomposition pathways. These changes to food webs can result in alterations to nutrient cycling pathways and shifts in carbon allocation within plant communities, which will further influence ecosystem dynamics.

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## **1 Introduction**

One of the long-standing and key questions in ecology is concerned with understanding how environmental factors influence species distributions and the assembly of communities. Much work has been done on this topic, however within the last several decades the looming threat of climate and land-use changes have spurred interest in how changes in these determinants will affect future communities and the consequences these changes will have for ecosystems and their functioning. Most attention has been on the effects of increased concentrations of CO<sub>2</sub> and subsequent increases in mean annual temperatures (e.g. Morgan et al. 2011; Eisenhauer et al. 2012), but a growing body of research is examining the effects of changing precipitation regimes on terrestrial ecosystems, focusing especially on changes in moisture availability for plants and soil systems. Plant systems have been the beneficiary of much of this research (no doubt in part due to their integral role as the source of energy within ecosystems), however the importance of understanding these dynamics for soils and their diversity has increasingly been recognized over the last decade. With this dissertation, I provide an overview of soil biodiversity and its role in ecosystems, a review of the current state of knowledge on the effects of altered moisture regimes on temperate ecosystems and a cross-site experimental study of the effect of changing moisture availability on soil communities within and along a large-scale climate gradient. To complement this experiment, I also present the results of a structural equation modeling approach to explore the direct and indirect effects of changes in soil moisture availability on mite and nematode communities.

## **1.1 Overview of soil biodiversity**

Soil systems are extremely biologically diverse and the large number of described species is thought to be only a fraction of total species diversity (e.g. Walter et al. 1996; Bloemers et al. 1997; Brussaard et al. 1997; Lawton et al. 1998), which has led to soils being referred to as the “poor man’s tropical rainforest” (Usher et al. 1979). This great diversity supports numerous ecosystem functions, the most important of which are decomposition and nutrient cycling. Soil communities are intimately tied with aboveground systems as a consequence of the services they provide as well as through their dependence upon plant productivity and organic matter inputs to the detrital food web (Coleman et al. 2004; Bardgett 2005). In chapter 2, I present an overview of the diversity of soil communities and their linkages with aboveground systems, as well as the services soil biodiversity provides and the implications future climate and land-use changes may have for these systems.

## **1.2 The role of moisture availability in temperate ecosystems**

Moisture availability is an important variable that controls plant growth and provides habitat space for soil organisms and facilitates ecosystem functions carried out within soils such as decomposition. Over the past two decades, research into the effects of changes to moisture availability and precipitation patterns has provided data on the responses of plant and soil communities that may provide insight into the dynamics of future ecosystem states due to climate change. With chapter 3, I review the literature from temperate forests, grasslands and desert systems and provide a summary of studies for plants and soil organisms, as well as highlight ways in which future studies can be improved in order to increase our understanding of how ecosystems may respond to future changes.



### **1.3 Effects of moisture availability on soil animal communities**

Soil communities are extremely diverse and participate in a range of ecosystem functions such as carbon storage, decomposition and nutrient cycling. Despite this role, it is unclear how soil communities may respond to changes in moisture availability and whether this might affect ecosystem functioning. In chapter 4, I examine the effects of changes in soil moisture regimes on communities of mites and nematodes, two highly abundant and diverse groups of soil animals, across a regional/global climate gradient comprised of a mesic and xeric grassland and a hot and polar desert. To further explore the role moisture availability plays in structuring soil communities, I present a structural equation modeling analysis of the effects of soil moisture availability and trophic interactions within soil animal communities in chapter 5.

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## **2 Linking soil biodiversity and vegetation: Implications for a changing planet<sup>1</sup>**

### **2.1 Summary**

Soil biota are intimately tied to plant communities through herbivory and symbiosis and indirectly by the decomposition of dead organic plant material. Through both roots and aboveground organic material (e.g. leaves and wood), plants provide substantial inputs of organic matter to soil systems. Plants are the basis for most biotic soil food webs that comprise an enormous diversity of species whose multiple interactions function to help regulate nutrient cycling, which in turn influences plant growth. Many factors govern the biogeography of soil biota, including the physical and chemical properties of soil, climate, the composition and type of vegetation and interactions with other soil biota. Despite awareness of factors influencing soil communities, no single factor allows predictions of soil animal diversity or distribution. However, research is showing that plants can have unique soil biotic communities. Degradation of soil removes predators and biotic regulation that occurs in less managed ecosystems and can result in increased pathogens and pests affecting humans, other animals and plants. Global changes such as land use, desertification and soil pollution all have been shown to alter soil animal diversity and abundance. Due to our dependence on soils and plant production, studies linking soil biotic communities to primary productivity are needed to assure long-term soil sustainability.

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## 2.2 Introduction

Plants and the biotic diversity beneath them are tightly linked, directly by soil herbivores, pathogens and symbionts, and indirectly through decomposition of dead plant material and return of inorganic nutrients to plants (Figure 2.1). For example, soil microbial symbionts (e.g. mycorrhizal and some free-living fungi and nitrogen-fixing bacteria) supply nutrients (such as P and N) to plant roots and are key to growth of many plant species. Herbivores that consume or parasitize plant roots are controlled in less managed ecosystems by species of invertebrates, fungi, bacteria and prokaryotes (Figure 2.1). These herbivores, including root parasites and pathogens, can reduce plant productivity or otherwise affect plant growth by influencing plant root architecture, plant metabolism, water and carbon transfer (Sasser and Freckman, 1987). However, many plant species have developed specific defenses against herbivores, including resistance genes against soil pathogens and parasites (e.g. viruses, bacteria, fungi and nematodes) (Hammond-Kosack and Jones, 1997). Decomposition indirectly affects plant growth through the recycling of nutrients by soil biota: dead aboveground and belowground organic compounds enter the soil and are transformed into inorganic nutrients over time by a succession of organisms working in concert (Figure 2.1). Bacteria and fungi break down cell walls and release nutrients, and larger invertebrates such as earthworms, termites and millipedes increase the surface area of leaves and twigs for smaller invertebrates to decay, thereby promoting decomposition (Coleman et al., 2004; Bardgett, 2005). These processes of symbiosis, herbivory and decomposition carried out by soil biota influence plant productivity and the soil habitat as well as hydrological and biogeochemical cycling.

Soils and their biota are essential to the regulation and performance of global biogeochemical cycles (Cortez and Bouche, 1998; Hedlund and Ohn, 2000; Hattenschwiler and

Bretscher, 2001; Lorenz and Lal, 2009; Gessner et al., 2010; Wall et al., 2010). At local to global scales, soils are heterogeneous in structure and possess physical and chemical characteristics that have taken hundreds of years to form, each developed by legacies of geology, climate, vegetation and soil organisms. The vast concealed biodiversity within soil is fundamental to maintenance of plant production, yet soils as a living natural resource are often ignored in issues of global changes such as food security, desertification, and pollution that affect plant diversity, distribution and extinctions. Soil animals are known to provide many benefits or ecosystem services including soil fertility, biocontrol of plant pathogens and parasites, decomposition and nutrient cycling, water filtration, soil formation (Wall, ed. 2004; Decaens et al., 2006; Barrios, 2007; Dominati et al., 2010) and regulation of climate through carbon storage (Woodward et al., 2009) in addition to supporting production of food, fiber and fuel. The maintenance and performance of these services are integrated with the functioning of aboveground ecosystems and the continued well-being of human populations (MEA, 2005). Global changes such as increased greenhouse gas concentrations, nitrogen deposition, degradation of soils and changes in land-use patterns are resulting in alterations to the linked above- and belowground biodiversity, which have repercussions for global plant and food production, as well as our future environmental sustainability (Wall et al., 2010). There is considerable evidence building as to the impacts and feedbacks that global changes may (or may not) have on soils and their diversity, which we highlight in order to provide a context for inclusion of soils and their biota into scientific dialogue on issues surrounding global change and management of Earth's animal and plant biodiversity.

With this paper, we present a general introduction to soil invertebrate diversity and ecology and address two questions: a) How do soil animals influence nutrient cycling and does

this influence vegetation? and b) How might these relationships be altered under global change?

We provide examples rather than an extensive literature review and limit our discussion to soil invertebrates, although we recognize that soil vertebrates and microbes also have a major effect on primary production, decomposition and plant distribution (Bardgett, 2005; Coleman and Whitman, 2005; Bagchi et al., 2006). Our focus is limited primarily to the relationships of soil invertebrates with vascular plants, although many species of soil invertebrates also feed on algae and bryophytes (e.g. Simmons et al., 2009).

### **2.3 Overview of soil animal ecology**

*Soil animal diversity*—We have only rudimentary knowledge of soil animal diversity in a few ecosystem types (Brussaard et al., 1997; Wall and Virginia, 1999; Bardgett et al., 2005) making it difficult to estimate the true diversity of soil taxa (Lawton et al., 1996). Described soil species are estimated at approximately 8000 species of Collembola (Bellinger et al., 1996-2010), 30 000 species of mites (Walter et al., 1996; Behan-Pelletier and Newton, 1999) and 5000 species of nematodes (Brussaard et al., 1997), but estimates of total diversity for these groups suggest that these may be only a miniscule fraction of the true diversity in soils (Wall and Virginia, 1999; Walter and Proctor, 1999). Within terrestrial systems, the soil biota are probably the most difficult to survey because: a) the soil is a murky medium where in situ identification of most organisms is impractical; b) the magnitude of organisms – there can be hundreds of thousands to millions of invertebrates in a 10 cm deep m<sup>2</sup> sample; c) organisms are small in size and morphological changes within the life cycle of a taxon are also common, thus leading to their often being categorized strictly by body size (Nee and Lawton, 1996; Bradford et al., 2002); d) methods of sampling and identification are time-consuming and laborious; e) references to global and regional distributions are often taxon-specific, species level composition is rarely

discussed and an all animal, total soil biodiversity analysis has been unreasonable (Wall and Virginia, 2000; Coleman, 2008; Wu et al., 2009); and f) taxonomic expertise for identifying individuals and building a basis for life histories and ecological interactions is vanishing or gone (Ronquist and Gärdenfors, 2003). Like aboveground biota, soil biota have primarily been studied in temperate climates and agricultural systems (Allen et al., 1995; Boag and Yeates, 1998).

These obstacles have been difficult to overcome. Current classical characterization methods to differentiate soil animals from levels of phyla to orders are a crude measure for such a range of diverse biota. Even within single groups, morphological identifications using many specific characters are inhibited by the many taxa needing identification. Soil animals range in size from visible (such as millipedes, earthworms and termites) to microscopic (e.g. nematodes and mites). Microfauna (< 0.1 mm body width) are aquatic organisms that include nematodes, rotifers and tardigrades (Coleman et al., 2004), and are amongst the most abundant and diverse of soil animals. For example, 431 species of nematodes were recorded from a tropical forest in Cameroon (Bloemers et al., 1997), and averaged over  $2 \times 10^6$  individuals  $m^{-2}$  (Lawton et al., 1996). Mesofauna (0.2 to 2 mm body width) include microarthropods (mites and Collembola) and enchytraeid worms. Diversity of these groups is high, with 162 mite species within 3 suborders collected from a tallgrass prairie in Kansas (St. John et al., 2006a). Earthworms and insects such as ants or termites are the largest animals typically encountered within soil and are categorized as macrofauna (> 2 mm body width).

***Soil animals and plants***—This mass of species of soil animals are involved in direct interactions with plants as well as indirect interactions that occur between different groups of soil animals. Vegetation supplies three types of inputs to belowground systems that influence the animal–plant interactions: living tissues (roots), dead organic matter (roots and plant leaf/stem

litter) and root exudates (Figure 2.1). Living roots are primarily fed upon by herbivorous insects (such as root weevils and beetles), plant-parasitic microfauna and some mesofauna (e.g. plant-feeding prostigmatid mites). In contrast, many generalist feeders such as macrofauna consume dead litter tissue as they shred it into smaller fragments in situ or consume litter material along with soil particles and other soil organisms. Root exudates (amino acids, carbohydrates and other compounds released into the soil substrate by plants) are generally consumed by microbes, which are in turn consumed by representatives from all size categories of soil animals (Grayston et al., 1998; Bonkowski et al., 2000; Ruf et al., 2006).

Once dead plant-derived material enters the soil food web for decomposition (Figure 2.1), trophic interactions serve to move carbon through various levels of consumers. Depending on the quality (e.g. carbon, nitrogen and lignin) and quantity of the dead organic matter, decomposition can occur by two pathways. More labile material is degraded by the bacterial decomposition pathway, with bacterivorous microfauna consuming and thus regulating the abundance of bacteria (Bardgett and Wardle, 2003; Parton and Silver, 2007). Recalcitrant litter (twigs or material with high lignin content) is decomposed primarily by fungi and micro- and mesofauna that preferentially consume fungi. There are of course some taxa that are omnivores and graze on both fauna and microbes. Predation within soil food webs results in transfers of nutrients from fungi and microbes through higher trophic levels, and can occur either within size categories (i.e. predatory microfauna feeding upon other microfauna) or between a larger size category and a smaller one (i.e. predatory mesofauna feeding upon microfauna). Macrofauna such as earthworms, while not strictly predators, consume any organisms that may be within ingested soil and litter material. Nutrients excreted from living animals and the decay of dead animals are



also part of the decomposition process, which contributes carbon and nitrogen and other nutrients in forms available for plant uptake (Bardgett and Wardle, 2003; Bardgett, 2005) (Figure 2.1).

***Distribution of soil animals***—A hotly debated question has been whether species of soil biota are cosmopolitan or whether certain taxonomic groups of soil organisms, especially those > 1 mm body size have restricted biogeographic ranges (Finlay and Fenchel, 2004; Bachar et al., 2010; Nemergut et al., 2010). This is of interest not only from an ecological theory perspective but also from a practical management perspective. If soil animal species were ubiquitous, conserving hotspots of plant diversity would potentially preserve thousands of species of soil biota; however, if plant species have distinct belowground communities and a tight relationship between above- and belowground biota exists, other conservation options for plant and soil species might be considered. Although to date there has been no standardized global assessment to address this topic or to determine if theories describing species diversity aboveground (e.g. latitudinal gradients) are applicable for soil species, evidence is accumulating that soils and plants have some unique communities of microbes and invertebrates, many of which are rare (Bardgett et al., 2005; Fierer et al., 2006; Fierer et al., 2009; Wu et al., 2009; Chu et al., 2009). Soil biota operate at the micro (gram of soil) scale within larger (field, regional and global) scales. Belowground biotic patterns are complex; even in relatively homogenous systems such as agricultural fields, aggregations of nematode feeding groups differ over tens of meters (Robertson and Freckman, 1995). Clarifying issues of biogeography and scale are important to conservation and management of ecosystems above- and belowground and much research has crystallized on identifying the factors that determine the distribution of soil biota across ecosystems. Among the major determinants of invertebrate diversity are the soil habitat and vegetation.

*Soil physical and chemical factors*—Physical structure and heterogeneity of the soil habitat are regulated by the percent contribution of three soil particles: sand (2 – 0.05 mm diam.), silts (0.05 - 0.002 mm diam.) and clays (under 0.002 mm diam.) (Bardgett, 2005). Soil chemical factors also vary and include hydrology (e.g. water holding capacity and the rate of water infiltration), cation exchange capacity (an indicator of nutrient retention and general soil fertility), pH and availability of nutrients (C, N, P, etc.) and minerals (Bardgett, 2005). Pore spaces between soil particles differ in diameter and this variation in pore size contributes to the distribution of animals in soils (Nielsen et al., 2008), as larger-sized animals typically favor larger pores while smaller pores serve as refugia for animals of smaller body sizes to avoid predation: Elliott et al. (1980) found nematode growth to be greater in fine-textured soils compared to coarse-textured soils as the smaller pores in fine-textured soil provided refugia for amoebae to feed within. Upon emerging from these smaller pores, amoebae were preyed upon by nematodes, facilitating transfer of energy and nutrients through food webs. This suggests that soil type affects prey abundance for predators and the quantity of nutrients that would be available to plants.

Many studies of invertebrates, including in desert systems, have demonstrated the importance of soil moisture for biotic activity and distribution, especially the aquatic microfauna. In the polar desert of the Antarctic Dry Valleys, the three endemic nematode species appear to be distributed partially by relative soil moisture: the abundance of one species, *Scottinema lindsayae* Timm, 1971, a microbivore, declines with increasing moisture while populations of the two other species, *Eudorylaimus antarcticus* Steiner, 1916 (Yeates, 1970), an omnivore, and *Plectus* spp, a microbivore, increases with soil moisture (Treonis et al., 1999; Courtright et al., 2001). When soil moistures decrease beyond a certain critical point, nematodes, tardigrades and rotifers enter a

state of highly reduced metabolic activity, known as anhydrobiosis, and lose 99% of the bound water. Entering anhydrobiosis allows these animals to persist in soils that may be highly variable with respect to soil desiccation, enabling activity when conditions are favorable and persistence when conditions decline (Adhikari et al., 2009). This further illustrates the complexity of soil factors that affect animal distributions as many species have evolved adaptations to live in water-stressed soils.

*Soil animals*—The soil habitat can also be altered by many macrofauna through their burrowing actions (leading to their often being referred to as “ecosystem engineers”), which can indirectly alter distributions of other soil animals. As earthworms burrow through soil, they mix the various organic and mineral layers of soil, disrupting the habitat for many organisms (especially mesofauna such as oribatid mites) while also altering the physical and chemical characteristics of soil. Microfauna carry microbes and transfer them to other soil particles. In the short term, these modifications may have varying effects on abundances of micro- and mesofauna (e.g. McLean and Parkinson, 2000; Frelich et al., 2006; Migge-Kleian et al., 2006) and microfauna (Huhta and Viberg, 1999; Ilieva-Makulec and Makulec, 2002; Raty and Huhta, 2003; Tao et al., 2009), however over longer time-periods these impacts appear to be largely negative, decreasing populations of micro- and mesofauna and altering the soil habitat (Migge-Kleian et al., 2006). In contrast, nests of termites and some ant species may actually increase abundances of mites and nematodes (Wagner et al., 1997; Boulton et al., 2003) as well as support more diverse or distinct communities of soil animals (Noti et al., 2003; Cadet et al., 2004). Due to modifications to the soil habitat and disruption of distinct organic layers, modifications to the plant community may also be observed due to the presence of earthworms, especially in habitats where they are invasive (Pare and Bernier, 1989; Frelich et al., 2006).

*Vegetation*—Plant species identity, vegetation composition, physiology, chemistry and phenology all influence soil invertebrate community composition, but more research is needed to predict whether there are hotspots of belowground biodiversity. For example, Porazinska et al. (2003) in a grassland study found limited effects of plant species richness and photosynthetic pathway ( $C_3$  vs.  $C_4$  vs. mixed  $C_3$  and  $C_4$ ) on abundances and diversity of some soil biota, but stronger effects in structuring soil communities were observed due to plant species identity and resource quality (C:N). Others (Wardle et al., 2004; St. John et al., 2006a,b; Bardgett and Wardle, 2003) have found idiosyncratic relationships between plant species and soil animals. Tree species identity can influence the composition of oribatid mite communities (Sylvain and Buddle, 2010) as can ecosystem type: comparisons of birch woodland and heather moorland yielded greater species richness of mites in woodland sites that were reflected in oribatid mite composition (Nielsen et al., 2010). However, the most intensively studied factor regarding the distribution of invertebrates has been plant litter chemistry. The quality of decomposing plant material and the relative quantities of easily decomposed compounds (e.g. simple carbohydrates and proteins) as compared to complex structural compounds (e.g. cellulose or less easily decomposed lignin) can have strong effects on soil invertebrate community composition (Swift et al., 1979; Wardle and Lavelle, 1997; Ball et al., 2009).

Additional aspects of vegetation can influence distribution of soil invertebrates. For example, most research has investigated the distributions of soil invertebrates in the surface layers of soils rather than at rooting depth, which may severely underestimate both abundance and diversity of soil organisms. Rooting systems penetrate the soil to greater depths (Jackson et al., 1996), and the few studies that have examined greater depths show a diversity of animals present (Jackson et al., 2002). In the Chihuahuan desert of New Mexico, nematodes were

recovered from up to 12 m depth; 75% of nematodes were collected below 0.5 m from mesquite in playa while 99.7% of nematodes occurred above 0.5 m near creosotebush (Freckman and Virginia, 1989). In the same experimental research Silva et al. (1989) found fewer than 5 soil microarthropods  $\text{kg}^{-1}$  dry soil beyond 3 m depth, indicating differences in resources or biology between the nematodes and mites. These results highlight the need for further studies investigating distributions of soil animals to rooting depth in ecosystems as changes in vegetation cover may influence soil animal distributions and activity both vertically and horizontally throughout the soil profile.

#### **2.4 Soil animals and nutrient cycling**

Herbivory links aboveground and belowground systems, impacting the amount and quality of inputs to belowground systems as well as influencing aboveground plant species composition and growth. Root herbivorous nematodes can consume up to 25% of belowground production with subsequent effects on aboveground plant productivity (Ingham and Detling, 1984). Additionally, defoliated plants allocate more C to roots when infested with root herbivorous nematodes (Ingham and Detling, 1986; Waters and Borowicz, 1994; Culman et al., 2010) that leaks into the surrounding soil (Yeates et al., 1998). Further, root herbivores can control plant succession by decreasing plant species dominance, which results in increased plant species diversity (de Deyn et al., 2003) and which in turn may influence nutrient inputs (Suttle et al., 2007).

Plant decomposition in natural systems and plant herbivory in agricultural systems are particularly well-studied nutrient cycling ecosystem processes: together these demonstrate that soil biota are essential components of ecosystem functioning (Ayres et al., 2009; Gessner et al.,

2010; Nielsen et al., 2011). Studies manipulating soil food web complexity (both in situ and in mesocosm lab experiments) have revealed the role of trophic groups (composite groups of species sharing similar feeding habits) in regulating rates of these processes through grazing and predator-prey interactions (Anderson et al., 1983; Ingham et al., 1985; Wardle and Yeates, 1993).

As part of the decomposition process, another important ecosystem function is stabilization of soil carbon. Once belowground, the rate of humification (the conversion of carbon sources from compounds relatively available to soil biota into stable, more resistant forms that decompose less readily) slows the flux of CO<sub>2</sub> and other greenhouse gases into the atmosphere (Lavelle et al., 2006). In turn, microbes and soil animals are key players in the creation of soil aggregates that bind and contain carbon (Plante and McGill, 2002; Bossuyt et al., 2005; Six et al., 2006), locking this material away from further decomposition and increasing stability over longer periods of time (Del Galdo et al., 2003; Lavelle et al., 2006). Thus, carbon fixed by plants in aboveground systems is stabilized and retained in soil by actions of animals and microbes, which can be a potential means of mitigating the quantity of atmospheric CO<sub>2</sub>.

While some have considered that high species richness in soils leads to functional redundancy (i.e. multiple species perform similar roles in ecosystems) in ecosystem processes such as plant productivity, decomposition and herbivory (see Bengtsson, 1998; Andren et al., 1995; Hooper et al., 2005), there are several examples where species play specific roles in ecosystem functioning (Coleman and Whitman, 2005; Wurst and van der Putten, 2007). Nielsen et al. (2011) surveyed the results of 85 experiments representing 26 published papers to reexamine manipulations of species richness and measured aspects of ecosystem functioning such as litter mass loss, carbon cycling and nutrient turnover. The synthesis noted that the

positive impact of soil animals on carbon cycling could be attributed to: a) increasing surface area for microbial activity (shredding and fragmentation of litter); b) altering the C:N:P of litter, increasing the rate of decomposition (partial digestion by animals); c) mixing microbes and organic matter (animals moving litter into soil); and d) stimulation of the microbial community through predation (Swift et al., 1979; Seastedt, 1984; Ingham et al., 1985; Wardle, 2002; Bardgett, 2005; Cole et al., 2006). These modifications in soil animal species richness and community composition could influence carbon cycling due to direct species-specific effects and indirectly through alterations in biotic interactions. Chauvel et al. (1999) noted that loss of individual earthworm species, or changes in dominance between species can have dramatic changes on ecosystem conditions.

There is a caution to ecosystem functioning studies and species redundancy. The total invertebrates found in a soil will interact to provide many services and participate in several ecosystem functions, but it is unlikely that a single species will influence all services and functions that influence plant growth or composition at the same time or in the same manner. A species in soil may be redundant only when measured against gross cumulative functions. Research to elucidate the relationship of a species to an overall function such as herbivory or decomposition should consider additional, perhaps smaller, quantifiable measures that would capture the involvement of species in each different step for the function. For example, consideration of only one large functional relationship (such as nutrient cycling) misrepresents the role of multiple species involved in the numerous small component steps of nutrient cycling. The loss of leaf litter mass may involve a succession of hundreds of animal species with different specific temporal and spatial cues.

## 2.5 Global change and soil animals

Evidence indicates that soil animals are vulnerable to global changes (e.g. climate change, land use change, invasive species, pollution) and soil disturbance (Scheu and Schulz, 1996; Bardgett et al., 2005, Parrent et al., 2006). Soil animals have been shown to increase decomposition rates in temperate and tropical ecosystems and have neutral effects in cold and dry systems, which have implications for plant communities and carbon cycling (Wall et al. 2008). However, due to the lack of coordinated, standardized global experiments on soil biodiversity as well as the inadequacy of information on the vulnerability of species and the functions they perform, the magnitude and consequences of the loss of soil biodiversity for vegetation-related ecosystem functions is uncertain. Several studies have shown reduced soil biodiversity with global changes (Van de Bund, 1970; Decaens and Jimenez, 2002; Gans et al., 2005) although there are also examples of positive and neutral effects (see reviews by Wardle, 1995; Bardgett, 2005; Nielsen et al., 2011). Changes that impact the soil habitat directly and consequently soil animal diversity (with varying effects on plant growth) include trampling and invading species (Garay and Nataf, 1982; Ayres et al., 2008; Darby et al., 2010). Trampling can compact soil, alter soil hydrology and biotic composition while invading plants and invertebrates can affect soil chemical and physical parameters (Ayres et al., 2008; Darby et al., 2010).

Climate change and land use change are mediated by increasing greenhouse gas emissions to the atmosphere and disruption to soils, (e.g. excessive fertilizer use, plowing, erosion and paving), both of which affect the connection between soil biota and plants (Figure 2.1). These global change drivers can affect vegetation by altering species composition, range distributions, primary productivity, decomposition rates and the soil habitat by hijacking nutrient inputs, altering the soil chemical and physical characteristics as well as contributing to rates of



species extinctions. Additionally, processes and feedbacks that occur at smaller scales are disrupted, which can potentially lead to alterations in function and the development of new or novel ecosystems (Sesastedt et al., 2008). Here we discuss examples of changes to soil animal communities mediated by two global change drivers (climate change and land use change) and how these community shifts may result in feedbacks to the overlying vegetation.

***Climate change***—Anthropogenic climate change affecting temperature, precipitation and consequently soil moisture will have varying effects on the diversity, distribution and abundance of soil animals, particularly aquatic soil microfauna with narrow temperature ranges. Experimental drying of soils in the Mediterranean to simulate decreased precipitation resulted in lower abundances and richness of microarthropods, (Collembola and oribatid mites) than controls, while increasing soil moisture by experimental irrigation showed the opposite (Tsiafouli et al., 2005). Soil moisture in some ecosystems can be a stronger determinant of microrarthropod community composition than either vegetation or soil properties as shown for mesostigmatid mites in woodlands and moorlands (Nielsen et al., 2010). In Hungary, warming and drying of soil as might be expected from climate change had no effect on the abundance and richness of nematodes but shifted their dominance and community composition (Bakonyi et al., 2007). Responses of soil animals to changes in soil moisture are not consistent across taxa or habitats, however, as has been demonstrated by work in peatlands and forests in Finland (Laiho et al., 2001). Manipulations of temperature affected macrofauna (earthworms) and mesofauna: Briones et al. (2009) showed increased temperatures of 3.5°C reduced populations of microarthropods and earthworms and decreased earthworm diversity, while only enchytraeid abundances responded positively to warming treatments. These few examples illustrate that as for aboveground plant species and functional groups, the response of soil biota at local scales to

changes in temperature and precipitation will depend on the physiological and functional responses of a particular group of taxa.

Whether future distribution patterns of soil animals will be altered under global climate change is uncertain. Vegetation range shifts due to climate change have been demonstrated, with plant species ranges either contracting into more localized distributions or expanding into new areas (Walther et al., 2002; Parmesan and Yohe, 2003; McLachlan et al., 2005), and it is likely that similar effects on the distribution of soil fauna will be seen (Ayres et al., 2009; Van der Putten, 2010). The effects of temperature will not affect both aboveground and belowground systems at the same time: responses to soil temperature lag behind those of air temperatures, leading to a delayed response of the soil system (Gehrig-Fasel et al., 2008). This can decouple aboveground-belowground relationships between soil fauna and their plant species as soil animals may synchronize more slowly with changing aboveground species distributions (Ayres et al., 2009). Top-down controls (trophic interactions whereby predators control populations of a lower trophic group) on root herbivores could become disrupted, leading to unexpected responses such as increased densities of root herbivores that in turn affect plant growth or the composition of plant communities (Engelkes et al., 2008; van der Putten et al., 2010; van Grunsven et al., 2010a,b)

***Land Use Change***—Urbanization, unsustainable forestry practices and intensive conventional agriculture are examples of land use changes that can have effects on soil biodiversity. These land uses create mosaics across the landscape that have regional and global impacts on soils, plants, atmosphere and water.

Over the last century, human populations have moved to urban, from rural, areas (Grimm

et al., 2008). This has resulted in the expansion of cities and suburban areas, and with this expansion increased paving leading to changes in hydrology, soil erosion and increased temperatures; deliberately altered vegetative cover due to ornamental plant introduction (such as turfgrass planting for golf courses or other monocultures) and increased pollution, both aerial and deposited (Grimm et al., 2008; Styers and Chappelka, 2008). Investigations of soil animal communities along gradients from rural-urban centers have yielded mixed results: decreases in nematode abundances occur with increasing urbanization (Pouyat et al., 1994; Pavao-Zuckerman and Coleman, 2007), but no differences in the abundances and species richness of ants and microarthropods were found between desert and industrial areas or between residential and agricultural areas of Phoenix, Arizona (McIntyre et al., 2001). Urban areas may have greater earthworm biomass than rural areas, with earthworms improving nutrient cycling rates when present (Steinberg et al., 1997). Urbanization was shown to affect vegetation resource quality (such as by altering C:N or lignin content) and rates of decomposition (Cotrufo et al., 1995; Carreiro et al., 1999; Pouyat and Carreiro, 2003; Nikula et al., 2010), which can influence soil fertility.

Timber harvesting, whether for immediate economic benefit (sale of lumber and wood products) or to clear land for other uses (such as settlement or agriculture in the tropics) affects the ecosystem in several ways: within northern temperate forests, removal of the canopy alters microclimate of the soil and litter habitat, disrupts nutrient inputs and balances (Ballard, 2000), and harvesting machinery compacts the soil (Ballard, 2000; Battigelli et al., 2004). Each of these actions alters the ability of vegetation to recover, and in some cases can result in new plant communities becoming established, which further affects the soil environment.

Several harvesting methods exist for clearing forest, ranging from whole-tree harvesting and removal (most destructive) to more conservative methods such as strip logging and thinning. These methods result in varied responses to soil biota. Clearcutting can severely affect the soil and litter habitats in forests, although not all groups of soil animals respond similarly. In general, as intensity of disturbance due to harvesting methods increased, abundances of microarthropods decreased (Abbott et al., 1980; Bird and Chatarpaul, 1986; Malmstrom et al., 2009) while annelid (earthworms and enchytraeids) abundances increased (Malmstrom et al., 2009); removal of forest floor material (such as through intensive harvesting or burning) had strong effects on soil animal communities (Battigelli et al., 2004; Berch et al., 2007; Dechene and Buddle, 2009; Dechene and Buddle, 2010). In tropical forests slash and burn or clearcutting practices are sometimes used to replace trees with a monoculture such as soybeans. Such simplification of vegetation cover in these areas corresponds to a simplification of the soil faunal communities (Rossi et al., 2010) and greatly affects nutrient cycling rates by removing vital plant nutrients as well as increasing emissions of greenhouse gases, often through burning (Chen et al., 2010). Given evidence showing the contribution of soil animals to the regulation of nutrient cycling processes, alterations to soil animal communities could result in decreased nutrient availability to plants and thus decreased productivity and soil fertility (Figure 2.1).

Use of land for agriculture has been occurring for millennia, with the most fertile lands becoming centers of civilizations. With increasing populations demanding more food, marginal lands are becoming used, frequently requiring more inputs of synthetic chemicals. These practices and intensive conventional agriculture (for biofuels, forestry or food) have numerous consequences for soils. This reduction of existing biodiversity to one or a few plant species aboveground limits inputs to the belowground system, which is further exacerbated through

harvesting high-quality plant tissues (Figure 2.1). Tillage and use of fertilizers and biocides further disrupt soil animal communities, reducing predator populations and increasing their prey, resulting in changes to nutrient balances beyond those due to shifts in vegetation (Frampton and van den Brink, 2007; Sanchez-Moreno and Ferris, 2007).

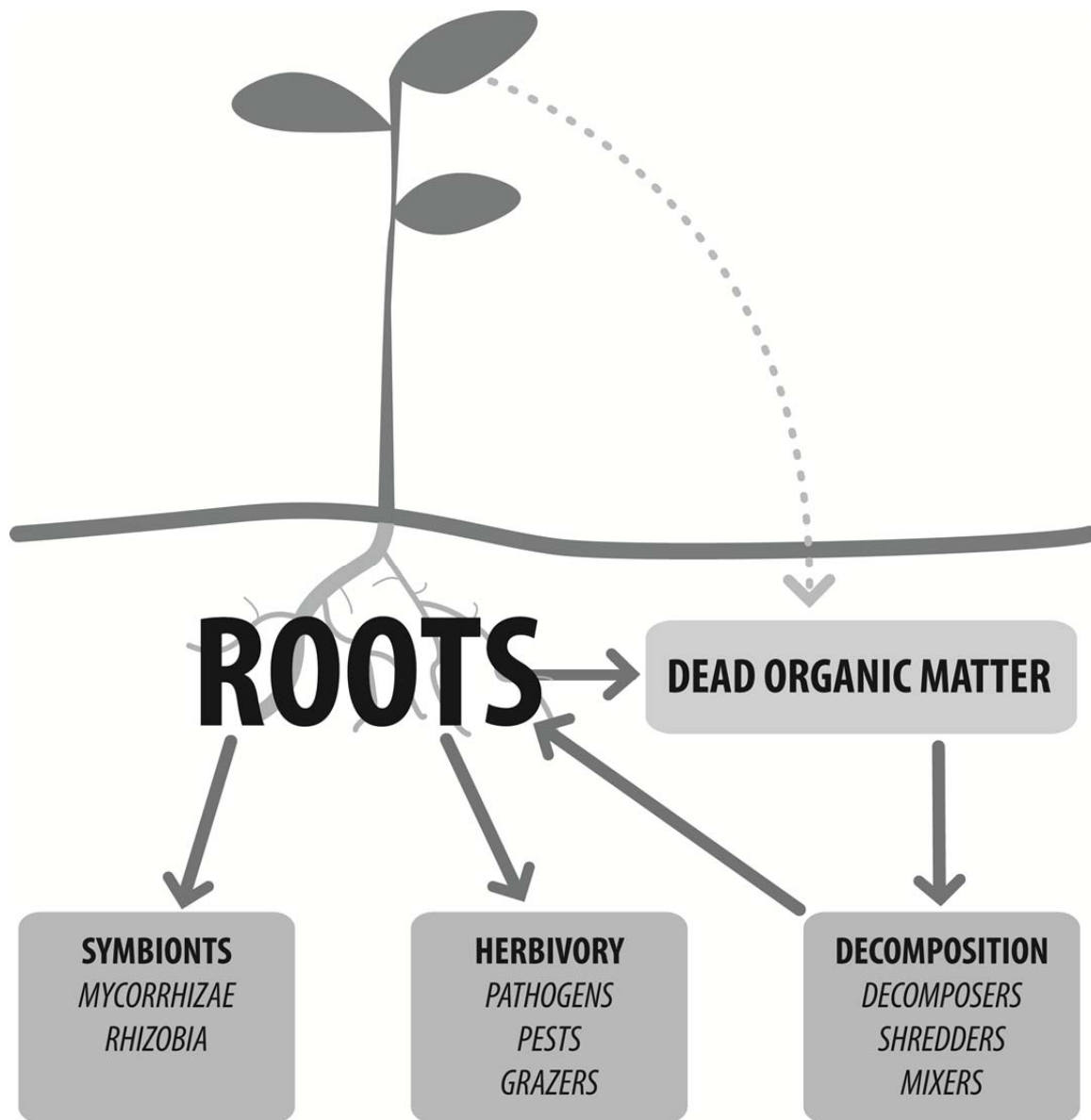
No-till (conservation tillage) or organic farming methods lessen disturbance to the soil substrate and generally reduce use of biocides, contributing to a more sustainable agricultural system. Studies on the effects of various tillage regimes have yielded mixed results for many groups of soil animals. For example, less destructive tillage regimes support higher abundances of earthworms and enchytraeids (Miura et al., 2008), microarthropods (Coleman et al., 2002; Eo and Nakamoto, 2008) and nematodes (Coleman et al., 2002; Overstreet et al., 2010) than conventional tillage, although other studies suggest otherwise. Responses of soil animal communities to no-till and conventional tillage regimes appear to be largely specific to taxon or functional group (Eo and Nakamoto, 2008; Miura et al., 2008; Sanchez-Moreno et al., 2009; Treonis et al., 2010), with variable changes in abundances and richness. This is especially true for plant feeding nematodes, which have been shown to be higher in no-till or reduced tillage systems than under conventional tillage (Govaerts et al., 2007; Overstreet et al., 2010), although in the case of the parasitic nematode, *Heterodera glycines*, densities declined with less frequent tillage (Westphal et al., 2009). These results may be due to changing tillage regimes, as altering between conventional and no-tillage or organic farming has been shown to have temporary effects on abundances of some plant feeding nematodes (Briar et al., 2007; Donald et al., 2009).

## 2.6 Conclusions

The linkages between soil animal diversity and vegetation are numerous and intricate, and in many cases are the result of associations with plant species that have arisen over millennia. Conditions in the ecosystems of Earth are changing rapidly, with rates of species loss seldom seen before. Research is quickly revealing the tight interdependence of soil biodiversity and aboveground systems and the many benefits, including economic, that soil biotic communities provide to human society.

The lack of awareness of the connection between land degradation and soil invertebrate biodiversity has been partially because soil science has traditionally focused on microbial processes such as nitrogen mineralization. In the past, biodiversity of microbial and soil invertebrates was unknown and complex, and research tools for exploration of species diversity and function were lacking. Today we are seeing significant research advances that should focus attention to management and protection of soil animal biodiversity. For example, we now know: a) considerably more about the diversity and abundance of species in soils and their interactions above- and belowground, b) that all species are not everywhere; there are biogeographic patterns for animals and microbes in soils, and, c) that multitudes of species of soil animals are involved in the biogeochemical and ecological functioning of terrestrial ecosystems. Because of these and other differences between above- and belowground biodiversity, conservation and management strategies aimed at aboveground systems may not work for the protection of soil animal biodiversity. A next step is to include knowledge of linkages between plant and soil biota in comprehensive biodiversity initiatives and policies.

As plant communities continue to be altered with climate change, their soil communities will become disrupted, with unpredictable feedbacks between these two systems. Research aimed at understanding the indirect and direct effects of climate change on soil organisms is fundamental to issues of food security and biodiversity management. New and tested tools used to illuminate functional groupings in soil ecosystems will improve our knowledge of food web dynamics and inform parameterization of decomposition and other models developed to investigate consequences of global changes and species range shifts. Global research based on soil habitats (Sanchez et al., 2009) can become a baseline observation system for temporal and spatial land use changes. Those in tropical countries and others who manage soil biodiversity for ecosystem services, particularly improved soil fertility, are providing quantitative information at regional scales (Moreira et al., 2008). New techniques will help determine how loss of soil biodiversity is tied to losses of function due to ecosystem-wide change and to associate shifts in species diversity with above- and belowground food webs. As global changes continue to alter the landscape and soils, integrating the latest research on above- and belowground biodiversity will help to manage ecosystems and maintain services upon which we depend.



**Figure 2.1:** Simplified diagram depicting pathways of nutrient flow between above- and belowground systems. Plant material enters soil food webs through roots and dead litter and serves to sustain complex communities of soil species. This biodiversity in turn converts nutrients into plant-usable forms through decomposition.



## 2.7 References

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### **3 The role of moisture availability in plant and soil communities of temperate ecosystems**

#### **3.1 Summary**

Terrestrial ecosystems are heavily influenced by climate factors, with species and biome ranges largely determined by the interplay of temperature and precipitation. Climate change models forecast alterations to temperature and precipitation regimes, which will affect moisture availability for plants and soil organisms. These changes may have important effects on several ecosystem services such as primary production and decomposition and nutrient cycling dynamics, and so understanding these effects is critical to helping us predict how terrestrial ecosystems will be affected in the future. We surveyed the literature on experimental and observational studies of the effects of moisture availability on communities of plants, soil microbes (bacteria and fungi) and soil animals in temperate forests, grasslands and deserts and present a review of the current state of knowledge of how moisture availability affects these organisms and ecosystems as well as a conceptual model to explain the strengths of these effects. A greater amount of research has focused on examining this relationship for plants than for soil systems and for changes in abundance, biomass or other growth metrics than for diversity. Plant studies demonstrate the clearest responses to changing moisture availability, especially along natural moisture gradients, while the effects on soil groups are less straightforward: increased moisture availability tends to have positive impacts on plant and soil microbial communities, while soil animal community responses are dependent on taxon or functional group. We suggest that including diversity metrics such as functional diversity in future studies may be useful to capture a higher-resolution perspective on the consequences of ecosystem change while utilizing existing sampling methods and infrastructure, and that including considerations to spatial scale may facilitate generalizability of results.

### 3.2 Introduction

Terrestrial ecosystems are strongly influenced by climatic factors such as precipitation and temperature, which help define biomes and climatic zones (Chapin et al. 2011). The interplay of precipitation and temperature helps to determine species range distributions and determine habitat suitability for terrestrial species at regional and continental scales globally. Both of these factors are being altered due to global climate change and while temperatures are expected to increase (IPCC 2007), changes to precipitation patterns are less straightforward and are likely to include changes to total precipitation amounts, alterations to the intensity of and duration between precipitation events and changes in the seasonality of precipitation (Easterling et al. 2000; Seneviratne et al. 2006; IPCC 2007; Smith 2011). These shifts in precipitation and temperature will influence soil water content, which in turn will impact above- and belowground productivity and diversity (Kramer and Boyer 1995; Griffiths et al. 2003; de Vries et al. 2012).

While precipitation, other climate factors and environmental legacies (e.g. geology) control plant species distributions and define biomes at large scales, soil moisture availability controls the direct influence of these factors on plants and soils by providing water for plant growth as well as affecting habitat suitability for soil organisms (Kramer and Boyer 1995; Bardgett 2005). Owing to the interplay of climatic (e.g. precipitation and temperature) and landscape factors (e.g. soil type, slope aspect), soil moisture availability at local and landscape scales can be highly variable through time and across space, which may be reflected in the different rooting strategies utilized by plants (Schenk and Jackson 2002a,b). This in turn influences the resource acquisition strategies of soil organisms at local scales: for example fungi create hyphal networks to access distributed resources (Boddy 1999). Soil moisture availability is the proximate factor that influences individual plants and soil organisms, as it reflects the

immediate habitat conditions to which these organisms are subject. Precipitation events are scattered throughout time, and the total amount of moisture that falls during any given event has only a short-term impact on the soil habitat as soils are able to capture and maintain only a portion of the total moisture from each event; some precipitation is lost through flow across the soil surface while moisture that cannot be maintained in soil pores is lost through infiltration down through the soil substrate (Kramer and Boyer 1995). Despite this, precipitation provides the source of recharge that replaces moisture lost from soils due to evaporation, losses due to percolation through the soil profile and losses due to plant usage, and so alterations to precipitation regimes will have important consequences for levels of soil moisture availability within ecosystems (Porporato et al. 2004).

Soil moisture therefore influences plant communities and plays an important role in primary production. In belowground food webs, this energy enters the food web through three primary channels (herbivory, bacterial and fungal mediated pathways) that converge at higher trophic levels (Moore and de Ruiter 2012). In turn, soil organisms provide numerous ecosystem services through their involvement in decomposition and nutrient cycling processes, as well as roles in soil development (Gessner et al. 2010; Wall et al. 2010; Sylvain and Wall 2011). Many soil organisms are aquatic, such as bacteria, protists and nematodes and are thus tightly tied to available soil moisture as a requirement for habitat space, however even microarthropods such as mites and springtails require a certain degree of soil moisture and will migrate throughout the soil substrate to avoid desiccation (Bardgett 2005). Key components of terrestrial systems are therefore dependent upon soil moisture availability and it is crucial to understand the dynamics that influence changes in soil moisture in order to understand how these communities will be influenced by climate change.

Research investigating how soil moisture availability influences terrestrial systems makes use of both experimental and observational methods. Experimental methods manipulating soil moisture availability include irrigation treatments (e.g. Silletti and Knapp 2001; Simmons et al. 2009) or drought simulations, with the latter being either complete and intercepting all incoming rainfall to be diverted away from research plots or partial interceptions that allow a proportion (such as 20% or 50%) of the natural rainfall amount to fall on plots (e.g. Yahdjian and Sala 2002). These treatments are applied to manipulate either the total amount of moisture that becomes available to the experimental setup while maintaining the frequency of natural precipitation patterns (mimicking current soil moisture recharge rates) or by manipulating the frequency (influencing precipitation variability) or timing (influencing precipitation seasonality) of events. Observational methods generally make use of either natural variation, such as between wet and dry years within a single site over a multi-year study, or by using gradients across elevation along hill slopes or across areas defined by different climatic conditions, such as semiarid steppeland into mesic grassland.

With this paper, we present a review of the effects of alterations to soil moisture availability on communities of plants and soil organisms, which form the foundation of terrestrial ecosystems. To address this topic we searched Web of Science for studies examining the effects of altered soil moisture availability on plants, soil microbes or soil animals (especially mites, nematodes and springtails), focusing on studies that examined changes in moisture availability from the perspective of altered precipitation regimes. We limited our focus to temperate forests, grasslands and aridlands, and include studies that examined changes in abundance (e.g. number of individuals, cover area, NPP, biomass and increases in leaf/root/stem length) and diversity (of both taxonomic and functional groups). Additionally, we further limited the studies to those that

collected data at the plot level (excluding greenhouse and bench-top studies), including gradient studies that aggregated plot-level data across several sites, yielding a total of 61 studies from peer-reviewed journals included in this review (Table 3.1). We provide both an overview of the current state of knowledge and a conceptual model regarding how changes in soil moisture availability impact plant and soil communities using data from both experimental and observational studies (Figure 3.1), as well as present a conceptual framework to explain why plant and soil communities differ in the strength of their responses to changing moisture availability by comparing direct and indirect effects (Figure 3.2). We also use these studies to highlight areas where our understanding of terrestrial responses to moisture changes are well documented, and emphasize areas needing further investigation.

### **3.3 Effects of moisture availability on plant communities**

Experimental manipulations of precipitation and soil moisture are frequently employed in order to investigate both above- and belowground responses of plant production (Table 3.1) as they enable the system of study to be pushed beyond natural variation or controlled in a manner that may reflect future conditions. One such method to accomplish this is through irrigation, where additional water can be used to supplement naturally occurring precipitation or where it can be added in different frequencies or different seasons to mimic potential changes in precipitation regimes. Increased moisture availability generally shows increases to plant productivity (Figure 3.1): for example, two grassland studies investigated the effects of irrigation on plant roots, finding increases to root length (Kreyling et al. 2008) as well as root biomass (Fiala et al. 2009) accompanying increased moisture availability, although in the latter study the results were site-dependent and observed only at highland locations. Site-specific effects were also observed in Spanish roadside embankment grass communities, with community cover

increasing with watering at one of two studied sites and responses to watering also showing species-specific patterns (Garcia-Palacios et al. 2012). Leaf elongation (a measure of NPP) of grasses increased in irrigated plots relative to controls on the Patagonian grassland of Argentina, suggesting that productivity is constrained by available soil moisture within this system (Golluscio et al. 1998). Additionally, two studies on grassland ANPP showed limited responses to irrigation, with changes to ANPP observed only in the first years of a two-year study in Wyoming (Skinner et al. 2002) and a three-year study in Oklahoma (Sherry et al. 2008). In this latter case the first year of the study was the treatment year and employed a doubling of ambient precipitation, with the following two years run as recovery years.

Precipitation exclusions are also a common method of manipulating moisture availability, and generally result in decreased plant productivity (Figure 3.1). Complete precipitation exclusions paired with “wet” and “dry” irrigation treatments of +/- 50% of long-term mean precipitation were used by Kardol et al. (2010a) in a multi-factor old-field study; treatments were run for two years in 2003-2004 and sampling of plant communities was carried out in 2006 and 2007, finding that biomass was 60-80% higher in previously wet vs. previously dry plots. Partial precipitation exclusions from plots are more commonly used, however, and have been employed in a variety of grassland systems. ANPP increased with irrigation and canopy cover decreased with drought in a single-year study in California (Potts et al. 2012), while a two-year spring and summer drought resulted in a 60% loss to plant biomass for temperate but not mediterranean sites in France (Poirier et al. 2012). In addition, single-year responses of plant production to drought have also been found: Yahdjian and Sala (2006) reported a decrease to ANPP with drought in the second (and final drought treatment) year of a three-year study, and Cherwin and Knapp (2012) reported decreases to ANPP in single years at the north and central sites of a two-



year, multi-site climatic gradient study of semi-arid grasslands in the southwest United States. Larger-scale (multiple plots per shelter) studies have also found similar results: in a large rainfall manipulation experiment in the semi-arid grasslands of Spain, Miranda et al. (2009) found that drought reduced overall biomass as well as the number of individuals within each plot, while another large-scale experiment in eastern Kansas found decreases in ANPP with drought (Fay et al. 2003). A grassland study in the United Kingdom utilizing both precipitation increases and decreases also found grass cover to increase with greater water availability while forb cover decreased (Morecoft et al. 2004).

Contrary to our general model of plant responses to changing soil moisture availability (Figure 3.1), not all studies manipulating moisture availability have found biomass responses to be tied to moisture increases or decreases, however, as a handful of studies found no relationship between moisture availability and plant productivity. In two grassland studies, no response of either above- or belowground productivity was observed to changes to moisture availability (Jentsch et al. 2011; Hoepfner and Dukes 2012), while in another study increases to ANPP with increases in moisture availability were counteracted by losses to belowground production (Dukes et al. 2005). Additionally, a manipulation of precipitation variability in a tallgrass prairie remnant found no effect of the experimental conditions on either grass or forb biomass (Derner et al. 2011).

Precipitation variability has been found to have effects in other studies, however: when maintaining the ambient amount of precipitation falling but increasing the duration between precipitation events, Fay et al. (2003) noted declines to ANPP were similar to those due to reductions in precipitation amounts under ambient patterning. Seasonality of precipitation also has influenced productivity: herbaceous biomass was higher when precipitation was added in

winter or under current patterns than when water was added in the spring (Bates et al. 2006). Additionally, the number or frequency of precipitation events can have strong effects on plant productivity, with a study by Heisler-White et al. (2008) finding that intermediate numbers of precipitation events (4 and 6) resulted in higher productivity than larger (12) or ambient (long-term average 14 events) patterns.

Examinations of natural variation in precipitation patterns have also revealed importance in the timing, distribution and amount of precipitation that falls on plant communities: much of this work occurred in grasslands, although examples from desert systems also exist. Interannual variability appears to be a strong driver of ANPP within two grassland systems (Konza Prairie, Kansas and Ukulinga Research Farm, South Africa), especially variability in late season precipitation at both sites (Knapp et al. 2006), and total ANPP at Konza Prairie appears to be best explained by the amount of precipitation or available soil moisture during the growing season (Nippert et al. 2006). Variability of precipitation between years also influenced perennial grass cover in the Sonoran Desert of Arizona, which was higher in wetter years (Munson et al. 2012), and the degree of precipitation and aridity controlled changes in shrub cover of in creosotebush shrublands (Munson et al. 2012).

The importance of timing or seasonality of precipitation appears to be common. Variation in the first half of the growing season was a good predictor of ANPP at Ukulinga, South Africa (Knapp et al. 2006), and at the Sevilleta grassland of New Mexico much of the variability in ANPP was tied to precipitation, especially to the timing and amount of summer precipitation (Muldavin et al. 2008). Suttle et al. (2007) found that winter addition plots responded similarly to ambient controls, but found strong effects on plant production when the rainy season was extended; increases to spring additions also resulted in community restructuring and a halving of

species richness by the end of the study. The Sonoran desert also responds to seasonality of precipitation, as increases to summer rainfall increased stem elongation in creosotebush more than spring or winter precipitation (Sponseller et al. 2012), and forb cover increased when exposed to winter precipitation amounts greater than 142 mm (Munson et al. 2012).

Additionally, the distribution of precipitation events, rather than the overall amount of precipitation has been shown to be a better predictor for ANPP at two grasslands in South Africa (Swemmer et al. 2007). In contrast, no effect of precipitation variability on grass ANPP was observed in a single study of the Patagonian steppe, although shrub ANPP showed some effect of short-term precipitation amounts in the same study (Jobaggy and Sala 2000).

A final approach to investigating the effects of moisture availability on plant productivity is through the use of natural landscape or climate gradients that provide a range of moisture amounts or natural variation in precipitation amounts. These studies make use of longer-duration climate patterns and show how ecosystems respond to more gradual changes in climate than those imposed experimentally, generally with more clear responses to changes in moisture availability (Figure 3.1). Both Barrett et al. (2002) and Zhou et al. (2009) found ANPP to increase with increasing mean annual precipitation along gradients in the United States, a pattern also observed in Inner Mongolia (Bai et al. 2008). ANPP isn't the only factor that is influenced by precipitation, however, as canopy height and leaf area have increased with precipitation across a gradient of seven national grassland sites in the United States (Lane et al. 2000). Gradient studies in non-grassland systems appear to be much less frequent, although two from forest systems have been reported. In Aleppo pine stands, total plant cover, height and volume increased with available rainfall (Osem et al. 2012), and fine root biomass decreased as available moisture decreased in mature beech forests in Germany (Meier and Leuschner 2008).

Less work has investigated the effects of water availability on plant diversity as compared to plant productivity, with the majority of studies being conducted in grasslands (Table 3.1). An irrigation study from the temperate steppe of Inner Mongolia found that increased precipitation increased the cover of both dominant and subdominant plants, as well as increasing the species richness of grasses, shrubs and nongrassaceous forbs (Yang et al. 2011). Decreases to species richness and diversity indices of grassland plants occurred in a drought study in Spain (Miranda et al. 2009), further highlighting the importance of moisture to plant diversity. Effects due to the variability of precipitation are less clear than those due to precipitation amounts, however: a three-year study in Kansas tallgrass prairie that decreased precipitation variability between years found no effect on either richness or diversity of grassland plants (Derner et al. 2011), while manipulating the frequency (but not amount) of precipitation had no effect on species richness or diversity in a grassland in Spain (Miranda et al. 2009). Despite these findings on precipitation frequency, the seasonality of precipitation does appear to be important, with winter (but not summer) precipitation amounts being strong predictors of herbaceous and grass species richness in a Texas grassland (Robertson et al. 2010).

Studies looking at natural variation of precipitation amounts indicate positive relationships between moisture availability and plant diversity (Figure 3.1). Gradients across Inner Mongolia (Bai et al. 2008) and western US grasslands (Adler and Levine 2007) found increases to species richness as mean annual precipitation increased, and the species richness of woody understory species of stands of Aleppo pine also increased with greater precipitation (Osem et al. 2012). Additionally, in a study examining how species climate envelopes might be influenced by changing precipitation regimes, Craine et al. (2011) found that decreases to precipitation could result in greater losses to native, rather than non-native plants.

### **3.4 Effects of moisture availability on soil microbial communities**

Manipulations of moisture availability for soil microbial communities generally follow similar methods to those used for plants, although these studies are much fewer in number than those for plants (Table 3.1) and show more idiosyncratic responses to changes in moisture availability (Figure 3.1); a single irrigation study manipulating total amounts of added water was found to fit the parameters of this review, and showed no effect of water additions on bacterial or fungal abundances in plots within the semiarid region of Inner Mongolia (Bi et al. 2012). Drought studies also report mixed results, with work from a dry heathland in Denmark reporting a decrease in microbial biomass with drought (although only at a depth of 6-9 cm; Stevnbak et al. 2012) and another study from an experimental grassland in Germany reporting increases to microbial biomass with drought (Jentsch et al. 2011). Additional studies looking at the abundance of microbial communities in response to changes in moisture availability indicate fungi (Hawkes et al. 2011) and PLFA concentrations (including bacteria; Gray et al. 2011) decrease as levels of available moisture increase.

Researchers have studied the effects of manipulating precipitation variability, either by altering the frequency of events or examining how drought affects soil communities in their response to rewetting events: rewetting of soil following a two-year drought treatment showed soil microbial biomass in the control treatments remained higher three weeks following rewetting than in the drought treatments, and bacterial numbers relative to those of fungi increased in drought plots as compared to controls (Landesman and Dighton 2011). Counter to this, the microbial component of biological soil crusts in arid lands were especially susceptible to alterations in precipitation variability, as manipulating the frequency and amount of precipitation

falling on experimental plots near Moab, Utah reduced the concentration of DNA in the soil crusts and lowered concentrations of cyanobacteria (Johnson et al. 2012).

In contrast to the idiosyncratic responses of soil microbial abundances to experimental manipulations of water availability, studies using natural gradients or other sources of natural variation tended to show a positive effect of increasing water availability on microbial biomass (Figure 3.1). Only one study, a vegetation gradient from native grassland into eucalyptus plantations in Argentina and Uruguay, found decreases in microbial biomass with mean annual precipitation (Berthrong et al. 2012). An additional negative response to precipitation was reported, but only for ectomycorrhizal fungi in stands of red pine to precipitation from the previous year; current year precipitation showed a positive relationship with fungal biomass (Okada et al. 2011). Forested systems have also been shown to have positive correlations between annual precipitation and bacteria and fungi, such as the relationship found for long-term mushroom yields in Switzerland (Buntgen et al. 2012). Other authors have found similar patterns along gradients extending across ecosystem types, with bacterial abundance (Bachar et al. 2010) and total soil PLFA concentrations (McCulley and Burke 2004) increasing with water availability.

Most studies of moisture availability on microbial diversity are conducted using natural gradients, although Hawkes et al. (2011) conducted a study using both drought and irrigation treatments, finding that as moisture availability increased there was a decrease to the diversity of fungal communities and that communities were much more variable than those found at lower moisture levels. Ordination and cluster analyses have shown microbial communities sort out by water availability: examples include bacterial and archaeal communities clustering by water content across a gradient in Israel (Angel et al. 2010), and regional clusterings of microbial

communities across a grassland gradient in the western US (McCulley and Burke 2004). Only a single study from a gradient in Israel suggests there is no link between microbial richness and precipitation (Bachar et al. 2010). The difference in the effect strength between bacterial and fungal communities may be due to bacterial communities being more susceptible to shifts in moisture availability, with fungi better able to adapt to changing conditions (Yuste et al. 2011).

### **3.5 Effects of moisture availability on soil animal communities**

Few studies overall have looked at the effect of moisture availability on soil animal abundances (Table 3.1), mostly focusing on either nematodes or microarthropods such as mites and springtails, but rarely all three taxa in a single study (although microarthropods are often studied together). Nematodes appear consistently to be regulated by water availability (Figure 3.1), although the degree to which individual species or functional groups respond varies: for example, in a drought study on Danish heathland, nematodes decreased with drought, albeit only at the surface (0-3 cm) layers of soil (Stevnbak et al. 2012). Stronger effects of moisture availability on nematodes were observed by simulated drought in an old-field system, which reduced nematode abundances in the top 10 cm of the soil (Kardol et al. 2010b) and in the organic soil horizon (0-3 cm) of the pinelands of New Jersey (where irrigation treatments also increased nematode numbers; Landesman et al. 2011), although in both cases the response varied by trophic group. Kardol et al. (2010b) found that while bacterivorous, fungivorous and root endoparasitic nematodes responded to drought, root hair ectoparasitic nematodes did so only when also subjected to elevated temperature; however, in the study by Landesman et al. (2011) the drought effect was only observed for bacterivorous nematodes, with other nematode trophic groups showing no response to the treatments. Overall amounts of water availability may be

important for nematode communities, but Darby et al. (2011) found no effect of manipulating precipitation variability on nematode abundances Colorado Plateau desert soils near Moab, Utah.

In contrast, responses of microarthropods (mites and springtails) to moisture availability are less clear than those of nematodes (Figure 3.1). Of four studies on springtails, two found no effect of moisture availability on springtail numbers (Irmeler 2006; Kardol et al. 2011), while two other studies found that wetter conditions increased the number of springtails (Tsiafouli et al. 2005; Chikoski et al. 2006). Two irrigation studies found differing effects on mite abundances, with irrigation in trembling aspen forest increasing mites (Chikoski et al. 2006) but irrigation in a tallgrass prairie site decreasing mite abundances, although this was driven by changes in prostigmatid mite numbers, with no response of oribatid mites observed (O’Lear and Blair 1999). An additional study incorporating both irrigation and drought treatments in plantations of Turkish pine found no effect of the individual treatments relative to the controls, however mite numbers did increase with greater moisture availability when comparing wet and dry treatments (Tsiafouli et al. 2005), and the frequency of precipitation events appears to be important in controlling numbers of prostigmatid mites in the desert of the Colorado Plateau (Darby et al. 2011). No effect of manipulating water availability on mite numbers was observed by Kardol et al. (2011) in an old-field system, and natural variability over 7 years in a beech forest also did not appear to correlate with shifts in mite abundances (Irmeler 2006).

Few studies exist on the effect of changes in moisture availability on soil animal communities and their diversity (Table 3.1), and responses appear to be taxon-specific (Figure 3.1). Nielsen et al. (2010) examined the role of environmental factors in a paired birch woodland/heather moorland study across Scotland and found that precipitation amounts explained more variation in mesostigmatid community composition than did vegetation or soil



properties. Additionally, irrigation patterns have been shown to influence microarthropod communities, with more frequent irrigation increasing evenness and diversity of springtails and less frequent irrigation increasing evenness and diversity of oribatid mites (Tsiafouli et al. 2005). Effects on the diversity of nematode communities are less clear: a drought study in Danish heathland found no effect on nematode trophic group diversity (Stevnbak et al. 2012), however irrigation had differential effects on nematode trophic groups, with herbivorous nematodes increasing 90% with water availability and idiosyncratic effects to fungivorous and microbivorous nematodes (Todd et al. 1999).

### **3.6 Response variation in plant and soil communities to changing moisture availability**

The clearest impacts of alterations to moisture availability on terrestrial ecosystems appear to be within plant communities, which is most pronounced in studies along natural gradients (Figure 3.1). Natural gradient studies also showed the clearest links between moisture availability and communities of soil animals and soil microbes (Figure 3.1), with largely positive relationships for microbial abundance and biomass and positive but taxon or functional-group dependent responses of soil animal communities; in all cases the responses from experimental manipulations were less clear or lacking altogether for the organisms covered in this review. The role of soil moisture availability on diversity appears to be clearer for plant communities as well, with consistent positive effects of increased moisture; soil animals also show positive effects of higher moisture availability, although these are weaker in effect and dependent upon the taxon or functional group being studied. Diversity of soil microbial communities appears to respond negatively to increased moisture availability, however community structure appears to be distinctive at different levels of moisture.

We propose that the magnitude and consistency of the responses of plant communities to changes in moisture availability may be greater than those of soil communities due to a difference in the relative importance of direct versus indirect effects in these two systems (Figure 3.2). Within plant communities, the direct effects of changing soil moisture availability influence resource availability—soil water provides plants with both moisture for growth and development of the organism as well as a primary component for photosynthesis, which provides for metabolic needs of the organism (Figure 3.2) and subsequently for terrestrial food webs. In contrast, the direct effects of soil moisture availability on soil communities are associated with habitat space, as soil organisms are either aquatic or require a certain threshold moisture value in order to survive (Figure 3.2). Soil communities are also affected by changing soil moisture availability indirectly through plant communities, with alterations to soil moisture availability first influencing plant production and root exudation, the products of which are used by belowground communities as the resources at the base of the food web (Figure 3.2).

Under this framework, it appears that changing resource availability is the most important factor for plant and soil communities affected by changing soil moisture availability. Although habitat space is no doubt important to soil organisms, many taxa have evolved methods to persist despite unsuitable habitat conditions caused by aridity: for example, nematodes have been observed to enter a state of dormancy called anhydrobiosis until conditions improve (Freckman et al. 1987; Treonis et al. 2000; Adhikari et al. 2009) and bacteria are capable of persisting under dry conditions through the formation of spores (although this is not always a requirement for drought survival: Chen and Alexander 1973). Other organisms are able to exploit moister portions of the soil habitat, either by greater mobility (such as microarthropods) or through growth into moister areas (such as by fungi). In this way, soil organisms are able to escape or

otherwise persist despite decreases to soil moisture availability, however these adaptations do not facilitate feeding in order to acquire energy for growth, development and reproduction. As a consequence, while the direct effects of soil moisture availability are strongest for plant communities (resource availability), the direct effects for soil communities (habitat space) are less important than those mediated by the indirect effects (resource availability from plant communities).

### **3.7 Future considerations**

*Integrating abundance and diversity* - More research has focused on determining the effect of changing moisture availability on plant abundance and biomass than on responses of belowground organisms (Table 3.1). This is due largely to several factors, particularly the relative ease with which ANPP or plant cover can be estimated for plants as compared to abundances of soil organisms, which are microscopic (or nearly so) and require more intensive effort to isolate from the soil substrate in order to be quantified. The focus of research on abundance of organisms as a response variable (as compared to diversity) is not unique to plants; of the literature surveyed for this review more papers were found for the response of abundance to changes in moisture for all plant and soil groups as compared to those quantifying diversity changes (Table 3.1), likely because estimating diversity (especially belowground) is labor intensive and requires specialized training to discern one species or group from another.

The lack of attention paid to diversity changes in ecosystems is unfortunate, especially as many ecosystem functions may be driven by a diverse assemblage of organisms rather than by the sheer number or biomass of organisms present in both above- and belowground systems. Plant production is supported by a host of interactions involved in converting senescent plant

material and dead organisms back into plant-available nutrients (Gessner et al. 2010; Wall et al. 2010; Sylvain and Wall 2011), and diversity of plants being monitored for productivity is important as numerous functions such as nitrogen fixation and differences in water use and carbon fixation strategies play a role in overall ecosystem functioning (Chapin et al. 2011). Within the soil, too, not all organisms contribute equally to all ecosystem functions, and there is a widening gap in our knowledge due to lack of attention to soil diversity. For example, the nitrogen cycle in soil features a complex suite of functions performed by microbial communities, and decomposition processes feature a variety of soil animals involved in breaking material into smaller components as well as in stimulating microbial activity through grazing activity (Bardgett 2005; Gessner et al. 2010). Full trophic webs within soil communities also function to partition energy throughout several trophic levels, and energy inputs to the soil range from being sourced from decaying organic material to direct exploitation of plant-derived carbon and nutrients through herbivory (Moore and de Ruiter 2012). Obtaining finer-resolution data on both diversity and function of soil organisms is facilitated by new technologies that have been developed in recent years, such as those used to determine the distribution and diversity of soil animals (Wu et al. 2011) and the diversity and function of soil microbial communities across several biomes (Fierer et al. 2012) globally, and these molecular techniques may see more widespread use, especially as costs per sample come down.

Given that much effort is already being devoted to establishing experiments and monitoring biota above- and belowground, it may be worth including diversity changes into a greater number of studies. While estimates of species-level diversity may be extremely time consuming, costly or otherwise difficult to obtain (or in some cases impossible, given taxonomic limitations), lower-resolution taxonomic diversity or more abstract diversity measures (e.g.

trophic or functional groupings) may still provide useful information on how ecosystems respond to change (e.g. Yeates et al. 1993; Bongers and Ferris 1999) without requiring specialized sampling methods or access to expensive instrumentation. Shifts in the contributions of functional roles in a community can provide important insight into future ecosystem states. For example, for plants, altering seasonality of rainfall could have unexpected and unbalanced effects on plant functional groups: increased spring rainfall resulted in an increase to nitrogen-fixing forbs in the first year of the study, followed by a subsequent increase in annual grasses that outcompeted most other plants in the plots and resulted in a halving to overall species richness (Suttle et al. 2007). Shifts in the contributions of soil functional groups have also been noted: changes in how nutrients and energy flow through trophic webs can be dramatically influenced by the relative contribution of organisms that feed upon bacteria, fungi or directly from plant roots (Moore and Hunt 1988). The interplay between the former two groups has important implications for nutrient cycling, as nutrient flows through bacterial pathways tend to be “leakier” than those through fungal pathways, resulting in greater losses of nitrogen (e.g. de Vries et al. 2011). For this reason, insight into how diversity changes and how biomass or abundances of different groups of organisms shift may provide important insight into how ecosystems respond to change.

*Considerations of scale* - An additional point of consideration for future research lies in addressing issues of spatial scale. Many studies are conducted within a single research site, which impairs our ability as researchers to make generalizations for regional or continental scales as many ecosystem processes operate across multiple scales, and may not be captured in a study focusing at only a single small scale (McGill 2010). The increased usage of meta-analytical techniques is helping to overcome limitations of the single-site study by standardizing

the strength of treatment responses and aggregate data across multiple experiments, however these fail to be able to account for differences in experimental design, environmental conditions and other factors that may vary between sites and across years. Investigations conducted only at regional or larger scales (such as when utilizing natural climatic gradients) can discern larger-scale patterns, but at the cost of losing resolution at local scales. For example, the global litter decomposition study conducted by Wall et al. (2008) investigated how the interplay of soil animal communities and climatic factors contributes to decomposition rates globally, and showed that soil animals have especially strong influence on decomposition processes within temperate and wet tropical regions. Designing experiments to bridge this divide between local/landscape and regional scales, such as that of Cherwin and Knapp (2012), where precipitation manipulations were established at three sites along a climate gradient within shortgrass steppe ecosystems, should be considered. In this study, site-specific responses to the treatments along the gradient, demonstrated that patterns found within individual sites cannot be generalized across the entire regional ecosystem type (Cherwin and Knapp 2012); other studies finding differing patterns between scales include Huxman et al. (2004) and Guo et al. (2012). These examples demonstrate that studies operating at more than one spatial scale can reveal not only how generalizable results from a single study site are to other sites, but also whether observed patterns are consistent across scales.

### **3.8 Conclusions**

With this review, we show that moisture availability is an important environmental variable in structuring not only aboveground, but also belowground terrestrial communities (Figure 3.1). Results from experimental manipulations appear to be less clear than those from studies using natural precipitation variation and natural gradients, which possibly suggests that

indirect effects of moisture have stronger influence on community abundance and diversity than does the direct influence of moisture availability alone (Figure 3.2). Given the likelihood of alterations to precipitation regimes facing ecosystems under global change scenarios coupled with increasing temperatures, the studies summarized here provide important knowledge on the responses of above- and belowground communities and the services they provide.

Ecosystems are likely to experience different changes to soil moisture regimes as a consequence of altered precipitation regimes: Knapp et al. (2008) propose that as precipitation patterns shift toward fewer but larger events, soil moisture availability may decrease in mesic systems but increase within xeric systems. This highlights the importance of examining how changing soil moisture availability influences communities across multiple ecosystem types, as studies from single ecosystems (such as grasslands) are unlikely to capture the full range of responses that will occur across the wide range of aridlands globally. Through our review of the existing knowledge of how a range of ecosystems respond and our suggestions for future research considerations we hope to demonstrate where our current state of knowledge is strongest as well as ways in which we can better improve our understanding of future dynamics across temperate terrestrial ecosystems.

**Table 3.1:** Studies fitting the criteria for inclusion within our review, noting response variables measured within the study, ecosystem type the study was conducted within, organisms of focus and type of moisture manipulation or observational study used. Studies followed by an \* indicate inclusion of organisms from multiple group types (e.g. plants and soil microbes or soil microbes and soil animals).

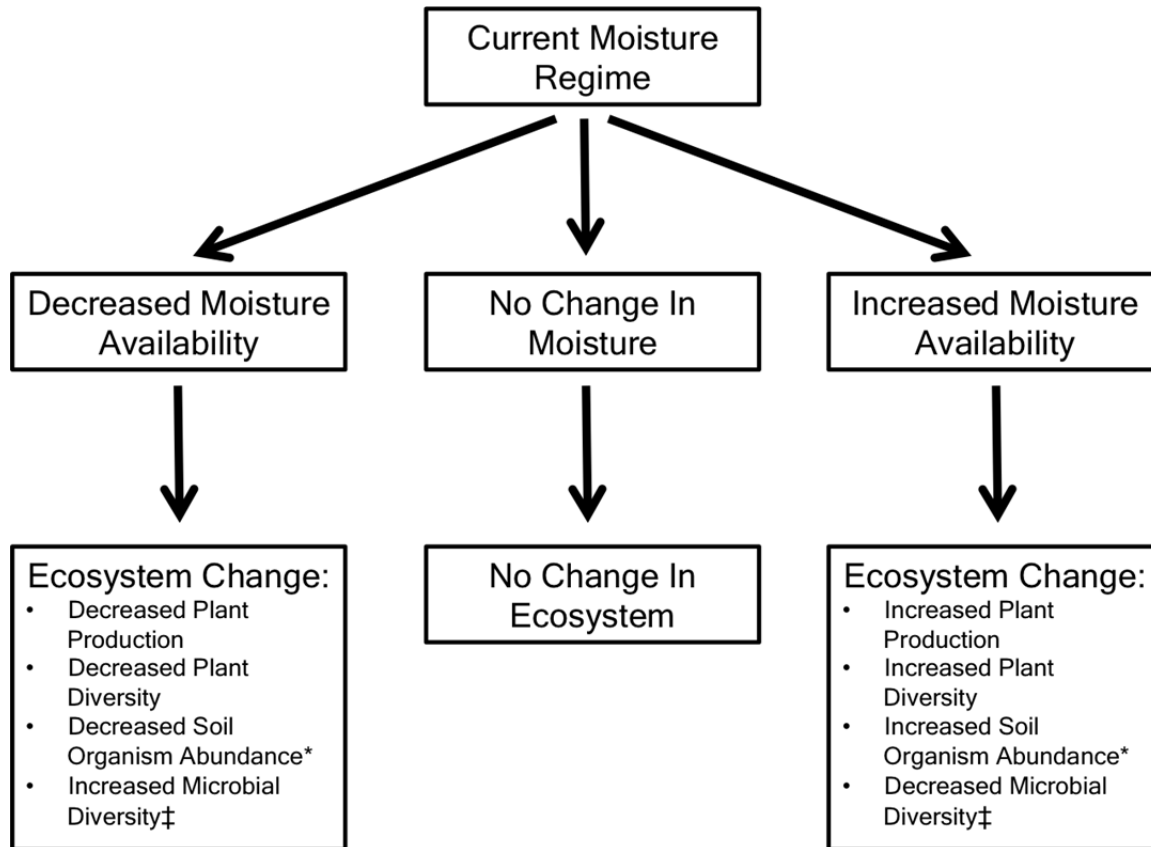
Reference	Response variable(s)	Plants		
		Ecosystem type(s)	Group of organisms	Study type
<i>Munson et al. 2012</i>	Cover area	Desert	Forbs, grasses, shrubs	Annual precipitation variation
<i>Sponseller et al. 2012</i>	Stem elongation	Desert	Shrubs	Annual precipitation variation
<i>Meier and Leuschner 2008</i>	Root biomass	Forest	Trees	Annual precipitation variation
<i>Osem et al. 2012</i>	Cover area, diversity, height, volume	Forest	Shrubs, trees, vines	Precipitation gradient
<i>Adler and Levine 2007</i>	Diversity	Grassland	Forbs, grasses, shrubs, succulents	Precipitation gradient
<i>Bai et al. 2008</i>	ANPP, diversity	Grassland	Forbs, grasses, shrubs	Precipitation gradient
<i>Barrett et al. 2002</i>	ANPP	Grassland	Grasses	Precipitation gradient
<i>Bates et al. 2006</i>	Biomass	Grassland	Forbs, grasses, shrubs	Precipitation seasonality
<i>Cherwin and Knapp 2012</i>	ANPP	Grassland	Forbs, grasses, shrubs	Drought, Precipitation gradient
<i>Craine et al. 2011</i>	Diversity	Grassland	Forbs, grasses	Climate envelope shifts
<i>Derner et al. 2011</i>	Biomass, diversity	Grassland	Forbs, grasses, shrubs	Precipitation variability
<i>Dukes et al. 2005</i>	NPP	Grassland	Forbs, grasses	Irrigation
<i>Fay et al. 2003</i>	ANPP	Grassland	Forbs, grasses	Drought, Precipitation timing
<i>Fiala et al. 2009</i>	Root biomass	Grassland	Forbs, grasses	Drought, irrigation
<i>Garcia-Palacios et al. 2012</i>	Cover area	Grassland	Forbs, grasses	Irrigation
<i>Golluscio et al. 1998</i>	Leaf elongation	Grassland	Grasses, shrubs	Irrigation
<i>Heisler-White et al. 2008</i>	ANPP	Grassland	Forbs, grasses	Precipitation timing
<i>Hoeppepner and Dukes 2012</i>	NPP	Grassland	Forbs, grasses	Drought, irrigation
<i>Jentsch et al. 2011*</i>	NPP	Grassland	Forbs, grasses	Drought
<i>Jobaggy and Sala 2000</i>	ANPP	Grassland	Grasses, shrubs	Annual precipitation variation
<i>Kardol et al. 2010a</i>	Biomass	Grassland	Forbs, grasses, shrubs	Moisture manipulation
<i>Knapp et al. 2006</i>	ANPP	Grassland	Forbs, grasses	Annual precipitation variation
<i>Kreyling et al. 2008</i>	Root elongation/biomass	Grassland	Forbs, grasses	Drought
<i>Lane et al. 2000</i>	Canopy height, leaf area	Grassland	Forbs, grasses	Precipitation gradient
<i>Miranda et al. 2009</i>	Abundance, biomass, diversity	Grassland	Forbs, grasses	Drought, precipitation frequency
<i>Morecroft et al. 2004</i>	Cover area	Grassland	Forbs, grasses	Drought, irrigation



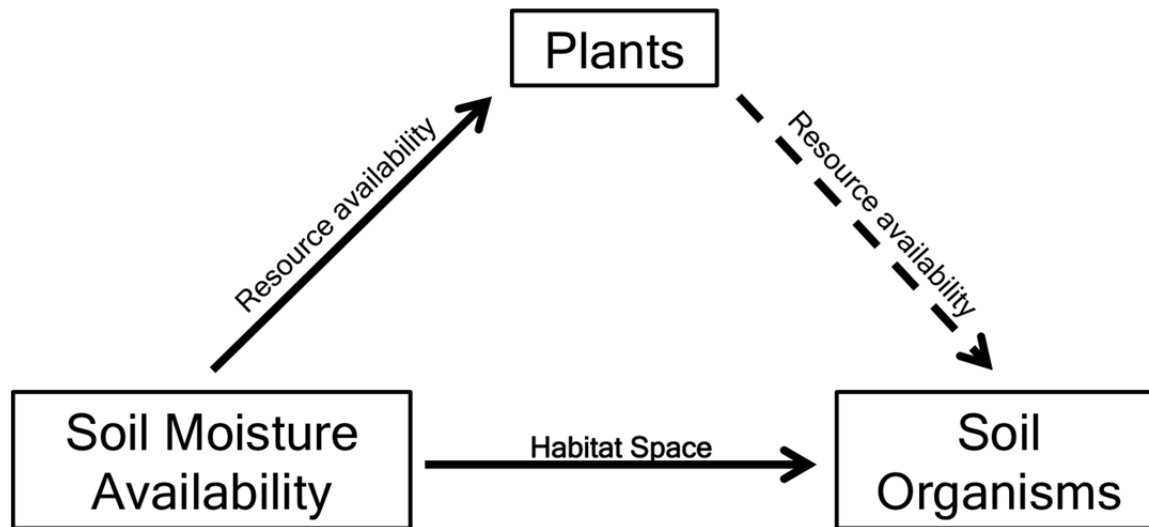
<i>Muldavin et al. 2008</i>	ANPP	Grassland	Forbs, grasses, shrubs	Annual precipitation variation
<i>Nippert et al. 2006</i>	ANPP	Grassland	Forbs, grasses	Annual precipitation variation
<i>Poirier et al. 2012</i>	Biomass	Grassland	Grasses	Precipitation manipulation
<i>Potts et al. 2012</i>	ANPP, cover area	Grassland	Forbs, grasses	Drought, irrigation
<i>Robertson et al. 2010</i>	Diversity	Grassland	Forbs, grasses, shrubs, succulents	Precipitation seasonality
<i>Sherry et al. 2008</i>	ANPP	Grassland	Forbs, grasses	Irrigation
<i>Skinner et al. 2002</i>	ANPP, root biomass	Grassland	Forbs, grasses	Irrigation
<i>Suttle et al. 2007</i>	ANPP, diversity	Grassland	Forbs, grasses	Irrigation, precipitation seasonality
<i>Swemmer et al. 2007</i>	ANPP	Grassland	Grasses	Annual precipitation variation
<i>Yahdjian and Sala 2006</i>	ANPP, density	Grassland	Grasses, shrubs	Drought, irrigation
<i>Yang et al. 2011</i>	Diversity	Grassland	Forbs, grasses, shrubs	Irrigation
<i>Zhou et al. 2009</i>	Biomass	Grassland	Forbs, grasses	Precipitation gradient
<b>Soil Microbes</b>				
<i>Johnson et al. 2012</i>	Abundance	Desert	Bacteria	Precipitation frequency
<i>Angel et al. 2010</i>	Diversity	Desert, forest, grassland	Archaea, bacteria	Precipitation gradient
<i>Buntgen et al. 2012</i>	Abundance	Forest	Fungi	Annual precipitation variation
<i>Landesman and Dighton 2011</i>	Biomass	Forest	Bacteria, fungi	Drought/rewetting
<i>Okada et al. 2011</i>	Biomass	Forest	EM Fungi	Annual precipitation variation
<i>Yuste et al. 2011</i>	Diversity	Forest	Bacteria, fungi	Drought
<i>Bachar et al. 2010</i>	Abundance, diversity	Forest, shrubland	Bacteria	Precipitation gradient
<i>Bi et al. 2012</i>	Abundance	Grassland	Bacteria, fungi	Irrigation
<i>Gray et al. 2011</i>	Abundance	Grassland	Bacteria, fungi	Moisture manipulation
<i>Hawkes et al. 2011</i>	Abundance, diversity	Grassland	Fungi	Precipitation manipulation
<i>Jentsch et al. 2011*</i>	Biomass	Grassland	Bacteria, fungi	Drought
<i>McCulley and Burke 2004</i>	Abundance, diversity	Grassland	Bacteria, fungi	Precipitation gradient
<i>Stevnbak et al. 2012*</i>	Biomass	Grassland	Microbes	Drought
<i>Berthrong et al. 2012</i>	Biomass	Forest, grassland	Microbes	Precipitation gradient
<b>Soil Animals</b>				
<i>Darby et al. 2011</i>	Abundance	Desert	Mites, nematodes	Precipitation frequency
<i>Chikoski et al. 2006</i>	Abundance	Forest	Mites, springtails	Irrigation
<i>Irmeler 2006</i>	Abundance	Forest	Mites, springtails	Natural precipitation variation
<i>Landesman et al. 2011</i>	Abundance	Forest	Nematodes	Drought/Irrigation
<i>Tsiafouli et al. 2005</i>	Abundance, diversity	Forest	Mites, springtails	Moisture manipulation
<i>Nielsen et al. 2010</i>	Diversity	Forest, grassland	Mites	Precipitation gradient
<i>Kardol et al. 2010b</i>	Abundance	Grassland	Nematodes	Moisture manipulation

<i>Kardol et al. 2011</i>	Abundance	Grassland	Mites, springtails	Moisture manipulation
<i>O'Lear and Blair 1999</i>	Abundance	Grassland	Mites	Irrigation
<i>Stevnbak et al. 2012*</i>	Abundance, diversity	Grassland	Nematodes	Drought
<i>Todd et al. 1999</i>	Abundance, diversity	Grassland	Nematodes	Irrigation

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**Figure 3.1:** Conceptual diagram showing projected changes to communities of plants and soil organisms as a result of altered soil moisture availability. Response strength is likely to differ between ecosystem types, and the magnitude and speed of the response for plant and soil communities is likely to be out of synchrony. For responses of soil organism abundance, \* denotes that these patterns are stronger in studies using natural climate or moisture gradients than those using an experimental approach to directly manipulate moisture availability and ‡ denotes that changes to soil organism diversity are taxon-specific.



**Figure 3.2:** Conceptual diagram showing direct (solid arrows) and indirect (dashed arrow) effects of soil moisture availability on plant and soil organism communities. For both plants and soil organisms, the strongest effect of soil moisture availability is due to changes in resource availability. Direct effects of soil moisture availability include water for growth and photosynthesis for plants and habitat space for soil organisms. Indirectly (as a result of effects on plant communities) soil moisture availability also provides leaf/root litter and influences root exudates that provide metabolic resources to soil organisms.

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## **4 Soil animal responses to moisture availability are largely scale, not ecosystem dependent: Insight from a cross-site study<sup>2</sup>**

### **4.1 Summary**

Climate change in much of the western US and other regions will result in a reduction in soil water availability either as a consequence of changes in precipitation or of increased temperature and evapotranspiration. How communities of soil animals such as mites and nematodes may respond to changes in moisture availability is not well known, and yet these organisms play important roles in decomposition and nutrient cycling processes. With this study we determined how communities of these organisms respond to changes in moisture availability, and whether common patterns could be found both along fine-scale gradients of soil moisture within four individual ecosystem types (mesic grassland, xeric grassland, arid grassland and polar desert) located in the western United States and Antarctica, as well as across a regional/global climate gradient of all four sites considered together. Within each of the four sites, an elevation transect consisting of three sampling plots was established, and soil samples were collected from these plots as well as from existing experimental manipulations of precipitation within each site once in fall of 2009 and three times each in 2010 and 2011. Mites and nematodes were then extracted, sorted to trophic groups, and analyzed to determine community responses to changes in soil moisture availability. We found that while both mites and nematodes increased with available soil moisture across the overall climate gradient, within individual ecosystems increases in soil moisture resulted in decreases to nematode communities at all but the hot desert site; mites showed no responses at any site. We suggest that communities

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<sup>2</sup> This manuscript will be submitted with additional co-authors: Karie L Cherwin, Debra PC Peters, Lara G Reichmann and Osvaldo E Sala.

of soil animals at local scales may respond predictably to changes in moisture availability regardless of ecosystem type, but that additional factors influence these responses over larger scales, possibly including aboveground diversity or community composition. Additionally, we found changes in proportional abundances of mite and nematode trophic groups as soil moisture increased within the individual ecosystem types, which may result in shifts within soil food webs with important consequences for ecosystem functioning.

## **4.2 Introduction**

Soil water availability is a major determinant of soil animal community composition and functioning, and climate change induced alterations in soil water will occur as a consequence of interacting changes to precipitation and temperature. Belowground ecosystems are affected by soil moisture controls on several aspects of soil chemistry including nutrient availability and leaching rates, and moisture availability, along with temperature, has also been shown to be an important driver of decomposition rates globally (Swift et al. 1979; Moorhead et al. 1999; Trofymow et al. 2002). Responses of communities of soil animals to shifts in precipitation regimes need to be studied to determine potential impacts to future ecosystem functioning (Blankinship et al. 2011; Eisenhauer et al. 2012).

Soil animal communities are extremely diverse, and include numerous groups of organisms such as mites and nematodes. These organisms make use of the soil habitat in different ways: mites inhabit the air-filled spaces between soil particles while nematodes are aquatic organisms that inhabit the water films located on the surface of soil particles (Coleman et al. 2004; Bardgett 2005). Responses of mites and nematodes to changes in precipitation and soil moisture availability are unclear: these groups are highly biologically and ecologically diverse (e.g. May 1988; Yeates et al. 1993; Walter et al. 1996; Bloemers et al. 1997; Walter and Proctor

1999) and it is unlikely that taxa, or the trophic groups to which they can be assigned, will respond in similar ways to changes in soil moisture. Trophic groups make use of the environment in fundamentally different ways, and changes at lower trophic levels (such as to microbial- or plant-feeding groups) may have large effects at higher trophic levels that influence energy, carbon, and nutrient flow through food webs (Moore and Hunt 1988).

The majority of studies examining soil animals have been conducted within a single biome, making comparisons between biomes difficult owing to differing methods in sample collection, isolation of animals, and method of identification (but see Heneghan et al. 1999, Gonzalez and Seastedt 2000, Wall et al. 2008 and Wu et al. 2011). Aboveground, plant communities vary in their sensitivity to water availability across biomes: wetter biomes such as tropical rainforests tend to have lower rain-use efficiencies than drier biomes such as deserts (Huxman et al. 2004). However, comparing multiple biome types often leads to commonalities in the response to drought (Huxman et al. 2004). Similarly, many studies of belowground communities were carried out within individual sites representing ecosystems. These studies provide useful information on how communities may respond to global change drivers (e.g., Tsiafouli et al. 2005; Bakonyi et al. 2007; Landesman et al. 2011; Eisenhauer et al. 2012), but few studies have compared multiple ecosystem types to reveal general patterns in the vulnerability of soil animal communities to global changes.

We investigated the impact that altered precipitation regimes may have on communities of soil animals. To address this, we examined the effects of changes in soil moisture on mite and nematode communities along a precipitation gradient across three grassland ecosystems in the central and southwestern United States, as well as an extremely arid polar desert system in Antarctica. The three grasslands included a mesic grassland, a xeric grassland, and a hot desert

(shrub-invaded grassland) to provide a gradient across arid lands, which comprise 41% of terrestrial ecosystems (MEA 2005). The Antarctic site provided both a location of extreme aridity as well as a polar comparison to the hot desert site. The objective of this research was to determine whether soil animal communities respond to changes in soil moisture regimes in a consistent manner across ecosystems and scales by using natural moisture gradients across different ecosystem types as well as experiments where precipitation was manipulated within each ecosystem.

We hypothesized that (1) patterns in moisture-induced changes to soil animal communities across the regional/global-scale precipitation gradient will be similar to those across the ecosystem-scale gradients within the arid and semi-arid sites (JRN, MCM, SGS) and (2) patterns along moisture gradients within the arid and semi-arid sites will show increased mite and nematode abundances with increasing moisture availability while those at the mesic site (KNZ) will show decreases. We expected that moisture-limited sites such as the semi-arid grassland and two deserts would have increased soil animal numbers as moisture availability increased because soil animals would be active for longer periods, rather than being tied to short activity periods following precipitation events (e.g. the Noy-Meir hypothesis; Noy-Meir 1973; Whitford et al. 1981). In contrast, at the mesic site we expected that moisture availability was sufficient even under the driest conditions to permit prolonged activity such that precipitation events shouldn't substantially impact habitat suitability. We also hypothesized that (3) nematodes will respond more strongly than mites to changes in soil moisture availability. Nematodes are aquatic organisms intimately tied to soil moisture availability to provide habitat space, while mites are better able to move throughout the soil habitat to access moister microhabitats. Finally we hypothesized that (4) animals at higher trophic levels will respond

more strongly than bacterial- and root-feeding animals, with fungal-feeding animals showing the least sensitivity to moisture. We expected that organisms at higher trophic levels (i.e. omnivores and predators) would be more sensitive to the changes at lower levels within the food web, responding strongly to moisture-influenced changes in prey availability (de Ruiter et al. 2005). Bacterial- and root-feeding animals should be next most sensitive given the dependence of plants and bacteria upon moisture availability in order to access resources for growth, with fungal-feeding animals being least sensitive given the ability of fungal hyphae to reach throughout the soil substrate and obtain resources from a larger area.

### **4.3 Materials and Methods**

*Site Descriptions* - Research was carried out along a broad-scale precipitation gradient encompassing four long-term ecological research (LTER) sites across the western United States and Antarctica, hereafter referred to as the cross-ecosystem moisture gradient (CEMG). The four sites ranged from wet to dry: three in the United States—Konza Prairie (KNZ), remnant tallgrass prairie near Manhattan, KS; Shortgrass Steppe (SGS), shortgrass prairie located northeast of Fort Collins, CO; and Jornada Basin (JRN), desert grassland north of Las Cruces, NM – and a fourth site in the McMurdo Dry Valleys (MCM), located in Taylor Valley, Victoria Land, Antarctica. Site coordinates, climate information and dominant vegetation can be found in Table 4.1, with soil information in Table 4.2.

*Experimental Design* - Within each of the four sites, a soil moisture gradient was created across an elevation transect to provide a natural range of variation at the landscape scale. Three 5 x 5 m plots were established along a hill-slope transect: one at the summit, one along the slope and the third at the base of the slope. Plots were selected to have similar vegetation cover type

(i.e., dominated by grasses, when present) within each LTER site, with samples being taken from under plant cover whenever possible. Sampling from bare ground was minimized except within MCM, where no vegetation cover is present. Existing experimental manipulations of moisture (generally an addition or reduction as a % of ambient precipitation) within each site allowed inclusion of extreme soil moisture values in order to determine how soil animals responded to conditions pushed beyond normal limits. These pre-established plots varied in size and water manipulation treatments (Table 4.3). This design allowed us to study patterns both within individual ecosystem types as well as across the CEMG.

***Environmental Variables*** - Several moisture-related environmental variables were used as proxies to assess soil animal community responses to changes in precipitation. Soil moisture was measured gravimetrically at the time of sampling by subsampling 50 g of the bulk sample used for nematode extractions and determining mass loss due to water evaporation after 48 hours at 105 °C (Barrett et al. 2008). Climate-related variables included annual precipitation from both the current and previous year, precipitation two weeks prior and over the current year prior to sampling, and aboveground net primary production (ANPP) for the current year, previous year and from two years previous, which were derived from data sets available on each LTER's web page (except MCM, where primary production and precipitation data were not available). Soil texture for KNZ and SGS was determined from datasets available on each LTER's web site while soil texture for MCM was obtained from Barrett et al. (2002) and from the NRCS web soil survey ([websoilsurvey.nrcs.usda.gov](http://websoilsurvey.nrcs.usda.gov)) for JRN.

***Sampling Methods*** - Soil sampling for nematode extraction and identification in the three US ecosystem types was carried out on seven occasions per site: once in fall of 2009 and three times each in 2010 and 2011, corresponding to before, during and after the wet season at each



site. Sampling in Antarctica was limited by logistics and length of the research season; it was conducted once annually for three years (2009, 2010, 2011) in the middle of austral summer for a total of 3 samples per plot. Samples for mites were collected from the final five sampling periods for the US sites. The sampling method for mites was changed after the second nematode sampling date in order to improve recovery rate of mites, with a larger diameter core used for the remainder of the study to minimize compression of soil edges (see below); mite data for the first two sampling periods were not used in analyses. No mite samples were collected from MCM owing to their extremely low densities and high patchiness within the Antarctic Dry Valleys (Adams et al. 2006).

Separate soil samples were collected for nematodes and mites to accommodate the differing extraction methods used for the two taxa. Soil cores measuring 10 cm-deep and 2.5 cm-diameter for nematodes and cores 10 cm-deep and 6 cm-diameter for mites were taken from all US sites. The extremely sandy and rocky soils at MCM are impractical for sampling with small-diameter corers; sampling for nematodes in Antarctica was conducted using sterile plastic scoops to collect soil to a depth of 10 cm and approximately 6 cm in diameter. For nematodes, bulk samples for each treatment were created by aggregating samples taken from 5 x 5 m plots along the elevation gradients within each site or from the smaller plots used for experimental precipitation manipulations. Eight soil cores were taken randomly from within each of the 5 x 5 m elevation gradient plots and for the experimental manipulations at KNZ, while single cores were taken randomly from within each of the smaller plots of the experimental manipulations at JRN, SGS and MCM. Because the experimental manipulations within JRN and SGS had only six replicate plots per treatment, an additional core was collected at random from two plots in each sampling period to obtain a total of eight cores per treatment. These bulk samples were returned

to the laboratory where they were subsampled for soil and invertebrate analyses under a laminar flow hood to reduce contamination. For samples from the experimental moisture manipulations at MCM, nematode abundances were averaged from the six individual plots extracted and counted separately for another study. Due to the high impact of disturbance from sampling and the extremely low rate of recovery, it was impractical to take additional samples specifically for this study without impacting the quality of the original study. Mites were extracted from single cores taken randomly within each 5 x 5 m plot for the elevation gradient within each site or from a randomly selected plot replicate for the experimental precipitation manipulations; these cores were not subsampled.

***Extraction and Identification*** - Nematode extractions were carried out using a sugar centrifugation flotation method (Freckman and Virginia, 1993). Nematodes were counted and sorted to trophic groups while live (see Yeates et al. 1993), within days of extraction and preserved in 5% formalin solution. Mites were extracted using modified Tullgren funnels (Crossley and Blair, 1991) with a heat gradient applied over the course of a week and collected into 70% ethanol. To maximize extraction efficiency, cores were split into two 5 cm depths prior to extraction. Mites were counted and sorted to trophic groupings of either mostly predatory (mesostigmatid and some prostigmatid mites) or generalists feeding on fungi, bacteria or detritus with some predators (oribatid and some prostigmatid mites) (Walter and Proctor 1999) and preserved in 70% ethanol.

Nematode trophic groups and mite suborders were used to compare commonalities in composition and ecosystem roles across sites. Nematodes were counted at 100-400X using an Olympus CKX41 inverted microscope, and mites were counted using a SZX9 dissecting microscope. Prior to all statistical analyses, nematode counts were standardized to numbers per

kilogram dry soil and mites were standardized to numbers per square meter. To facilitate direct comparisons of mites and nematodes, nematodes were standardized to numbers per square meter using bulk density data for soils from each site: 1.4 g cm<sup>-3</sup> (JRN; Monger 2006 and SGS; Heisler-White et al. 2009) and 1.5 g cm<sup>-3</sup> (KNZ; Heisler-White et al. 2009).

**Statistical Analyses** - For all analyses, mites and nematodes were treated separately. Regression analyses for the relationship between soil moisture and other variables with animal numbers were conducted using log-transformed data ( $\ln x + 1$ ) to satisfy the assumptions of normal data distribution and on data averaged over each year per plot. Additionally, analyses were conducted only on presence data (i.e. analyses excluded animal counts of 0) in order to examine the role moisture availability plays in controlling animal populations when present; this also allowed inclusion of data from MCM, where soil animals are represented by only two trophic groups (bacterial-feeding and omnivorous nematodes). Analyses on proportional abundances were conducted using untransformed data. For multiple regressions, model determination was conducted using a backward elimination method by comparing model terms for inclusion using analysis of variance testing. Models were simplified to exclude variables with correlation coefficients  $> 0.85$ . All statistical analyses were performed using R, version 2.11.1 (R development core team, 2010) with regressions conducted using the `lm` function of the default R package.

#### 4.4 Results

**Within-site and Cross-site (CEMG) comparisons** - Nematode numbers were generally high within all sites, although the dominant groups differed between sites (Fig. 4.1a, Table 4.4) and numbers of mites differed within each site where they were present, with generalist mites always more abundant than predatory mites (Fig. 4.1b, Table 4.4). The established treatments

had significant effects on nematode numbers within JRN and MCM, but no significant effects on soil animal numbers were observed within KNZ or SGS; within JRN experimental manipulations supported higher abundances than the soil moisture gradient along the elevation transect (Fig. 4.2a) while effects within MCM mirrored expected trends in soil moisture (Fig. 4.2b).

Mites and nematodes responded to moisture in different ways. Numbers of nematodes from all trophic groups decreased within sites as moisture availability increased, as did Shannon diversity and species evenness (Tables 4.5-4.7), except at JRN where no response to soil moisture or moisture-related variables was observed. No response of mites to moisture availability or moisture-related variables was observed within any of the sites in this study. In contrast, nearly all groups of soil animals (except for bacterial-feeding nematodes) increased across the cross-ecosystem moisture gradient (CEMG) as available soil moisture (Figure 4.3) and other moisture-related climate variables increased (Shannon diversity and species evenness decreased, Table 4.8), although all groups varied in the strength of their responses relative to the moisture and climate variables used (Table 4.8).

***Trophic Groups*** - Although no responses of mites to moisture or moisture-related variables was observed within any of the individual sites in this study, both mite groups increased with increases in these variables across the CEMG (Figure 4.3). The proportion of generalist mites increased relative to microbial-feeding nematodes (e.g. bacterial- and fungal-feeders) across the CEMG ( $R^2 = 0.93$ ,  $p < 0.0001$ ) and the proportion of predatory mites increased relative to omnivorous and predatory nematodes ( $R^2 = 0.98$ ,  $p = 0.0003$ ). Additionally, the overall proportion of mites increased relative to total nematode numbers ( $R^2 = 0.45$ ,  $p < 0.0001$ ).

All nematode trophic groups decreased with increases in soil moisture or moisture-related variables within the individual sites used in this study (except at JRN as previously noted), although changes in the proportional abundances of nematode trophic groups led to shifts in community composition. These changes were greatest at KNZ where large decreases in the proportion of bacterial-feeding nematodes were accompanied by a sharp increase in root-feeding nematodes with increases to ANPP two years prior to sampling (Figure 4.4a). At MCM, the proportion of bacterial-feeding nematodes sharply decreased with increases in available moisture and was paired with a sharp increase in the proportion of omnivorous nematodes (Figure 4.4b). Across all sites of the CEMG, the proportion of fungal-feeding, root-feeding and predatory nematodes increased with available moisture or moisture-related variables, and bacterial-feeding nematodes decreased. No response of omnivorous nematodes was observed relative to these variables (Figure 4.5).

#### **4.5 Discussion**

This study provides one of the first multi-site, cross-scale investigations of how soil moisture availability can control populations and communities of soil animals within several ecosystem types. We show that soil animals respond to changes in moisture availability and related factors in a largely similar manner regardless of ecosystem type, and that responses of these organisms differ between landscape and regional scales. Our findings demonstrate that at regional scales incremental increases in moisture availability at lower soil moisture values have a strong positive and nonlinear effect on soil animals, while across individual ecosystem types this effect is more gradual, linear and generally negative in its relationship.

*Within-site and cross-site (CEMG) comparisons* - One of the most notable findings in this study is the difference in the response between patterns observed across the CEMG as compared to the patterns observed within the individual ecosystems. Contrary to our first hypothesis, patterns of animal responses to changes in moisture observed across the CEMG did not match those found within any of the individual ecosystems; additionally and in contrast to our second hypothesis, responses within nearly all of the individual ecosystems were similar regardless of whether they were arid, semi-arid or mesic, with the exception of JRN. Across the CEMG, nearly all animal groups (except bacterial- and fungal-feeding nematodes) showed strong non-linear increases in abundance to moisture increases at low values of soil moisture availability with a threshold between 10 and 15% soil moisture, at which the response leveled out and approached an asymptote. This suggests that soil moisture controls are critically important at low levels of moisture availability, but that other factors become more influential once a critical point has been passed. Modeling studies investigating the interactive effects of temperature and moisture availability on nematode population dynamics in the Chihuahuan desert (Moorhead et al. 1987) and Antarctic polar desert (Weicht and Moorhead 2004) further support the importance of moisture availability for these organisms, as the long-term persistence of nematode populations in both of these ecosystems was due to these interactive effects controlling soil moisture availability and therefore habitat suitability. At low moisture thresholds, these models showed that nematode populations were able to persist despite unsuitable habitat conditions due to the ability of these organisms to enter anhydrobiosis and remain dormant until conditions improved (Moorhead et al. 1987; Weicht and Moorhead 2004). While we did not monitor the frequency of anhydrobiotic nematodes in our study sites, the non-linear responses of nematodes to moisture availability within our study show a sharp increase in the number of

individuals recovered that roughly corresponds to reported moisture thresholds below which nematodes enter anhydrobiosis (~4.7% soil moisture in the Chihuahuan desert, Freckman et al. 1987; and ~2% in the Antarctic polar desert, Treonis et al. 2000).

Threshold responses and differences in the directionality or strength of responses of organisms between multiple ecosystem types and larger scales (such as was found within this study) occur in aboveground systems: for example, Huxman et al. (2004) and Guo et al. (2012) show variations in response strength of grassland ANPP to moisture across scales. Guo et al. (2012) found increases to ANPP with increased MAP to be exponential between 300-500mm/year, although this response appears to gradually decrease in strength beyond MAP values of 500mm/year (Huxman et al. 2004). These two studies demonstrate that changes to moisture availability may be of greater importance to plants and soil organisms at low levels of moisture in aboveground systems as well, highlighting the need to consider whether ecosystems may be pushed beyond critical thresholds due to climate change-induced shifts in environmental factors.

Threshold responses are especially important to consider in the context of short-term events, which can have more immediate impacts than those due to long-term change both locally and regionally. For example, intensive grazing pressure in the arid southwestern United States may have helped to push the arid grassland systems over a tipping point, facilitating invasion by and conversion to arid shrublands, such as within the Jornada Basin (Whitford 2002; Bestelmeyer et al. 2006). Extreme climatic events may also contribute to pushing systems beyond critical thresholds: within the Antarctic Dry Valleys, an increase in the frequency of unusually warm summers results in greater glacial and permafrost melt that changes nematode community composition (Wall 2007; Nielsen et al. 2012) and can impact rates of C cycling

(Barrett et al. 2008). Additionally, a severe drought between 2000-2003 in the southwestern United States facilitated an outbreak of bark beetles in stands of Colorado pinyon pine, resulting in over 90% mortality at one site in New Mexico (Breshears et al. 2005), greatly altering the vegetation community of the area owing to its role as the dominant overstory species. These changes to ecosystems may become more common, especially considering that severe droughts similar to that of the Breshears et al. (2005) study and the drought affecting the midwestern United States in 2012 may occur with increasing frequency in the future (Easterling et al. 2000; Strzepek et al. 2010).

While environmental factors are fairly consistent within the individual ecosystem types (excepting slope aspect and plant productivity), several factors vary across the CEMG that may explain the different patterns in soil animal abundances and community composition observed between the CEMG and the individual ecosystems within this study: these patterns also include the influence of aboveground plant species identity, quality, and cover (Porazinska et al. 2003; Sylvain and Buddle 2010; Eisenhauer et al. 2012; Klass et al. 2012). Eisenhauer et al. (2012) suggest that root production and carbon allocation may drive changes in soil animal communities; they observed increases in N to limit carbon inputs to the soil through roots and a subsequent decline in animal richness. This may be especially informative in relation to drought, as plants have been observed to alter root architecture and production in response to soil moisture limitation (Schenk and Jackson 2002a,b). Aboveground diversity and species identity may also potentially explain the observed differences in patterns, as litter diversity (Hansen and Coleman 1998), litter quality (Garcia-Palacios et al. 2013) and plant species and functional group richness (Porazinska et al. 2003) can influence composition of soil communities. Moisture availability affects habitat suitability in soil, and is responsible for resource availability both



directly (root inputs) and indirectly by providing resources for microbial communities. At the global scale, Wu et al. (2011) note that belowground diversity does not track well with aboveground diversity, as high eukaryotic OTUs didn't occur in traditionally considered diversity hotspots (based upon aboveground diversity estimates). It may be that aboveground diversity plays a role in structuring soil animal communities at scales that are intermediate to global or local scales, and at these larger scales climate change will result in shifts to species ranges and biome distributions, which can potentially have large effects on environments at the local scale (Walther et al. 2002; van der Putten et al. 2010).

*Taxa and trophic groups* - Across the CEMG, mite and nematode trophic groups (with the exception of bacterial-feeding nematodes) responded similarly and increased in number with increases in soil moisture availability. Within the individual ecosystems, however, only nematodes responded to changes in soil moisture, with general decreases in all nematode trophic groups observed as moisture availability increased. No response of either group was seen in the hot desert, JRN. These results partially matched our third hypothesis that nematodes would respond more strongly than mites to changes in moisture availability, although only within three of the four ecosystems studied (MCM, KNZ, SGS) and not along the CEMG (where mite and nematode communities responded similarly) or within JRN (where neither group demonstrated a response to changes in available soil moisture) as we had predicted. Decreasing moisture has been shown to positively influence abundances of bacterial- and fungal-feeding nematodes (Wasilewska 1991; Yeates and Bongers 1999) and increases in root-feeders and omnivores have been observed with increasing precipitation (Yeates and Bongers 1999). However, decreases of all trophic group abundances with soil moisture increases within the two grassland ecosystems (KNZ and SGS) represent patterns not previously reported. In contrast to our fourth hypothesis,

the strength of responses of individual trophic groups to changes in moisture availability did not match expected patterns within each ecosystem or across the CEMG: while omnivorous nematodes tended to respond strongly to changes in moisture availability, predatory nematodes responded the least strongly and other nematode groups showed no clear order in the strength of their response. The lack of a response of any mite group to changes in moisture availability was also unexpected and contrary to this hypothesis.

Patterns in soil animal responses to changes in moisture availability within individual sites were unexpected: for example, changes in community composition, but not decreases in abundance, as a response to changes in soil moisture availability have been reported from MCM by Treonis et al. (1999) and Courtright et al. (2001). Within the wettest biome (KNZ), a decrease in nematode abundance with increasing moisture may have been observed because of prolonged habitat unsuitability due to oversaturation (although this was not measured), while the xeric grassland (SGS) may feature nematode communities that have been selected via environmental filters and adapted through time to more arid conditions. The lack of nematode responses within JRN to changes in moisture reflects findings of earlier research conducted at the same site (Whitford et al. 1981; Steinberger et al. 1984; Freckman et al. 1987). In this study, only changes in soil texture had significant effects on nematode abundances within JRN.

Both taxa responded similarly across the CEMG. Within individual ecosystems, however, only nematodes responded to changes in moisture availability; thus our third hypothesis is partially supported for changes in soil animal communities at the ecosystem scale. This reflects the different manner in which mites and nematodes make use of the soil habitat, with nematodes being more responsive to changes in soil moisture availability as a result of life-history traits tying them to an aquatic environment. Nielsen et al. (2010) suggest that annual precipitation

amounts may influence soil communities only at larger spatial scales and the results of this study confirm Nielsen et al, showing that this influence may vary at local and regional scales, with soil moisture being the most immediately important moisture factor at smaller spatial scales. The lack of mite responses to changes in moisture within the individual ecosystems of this study conflict with studies finding positive responses to increased soil moisture availability in individual ecosystems (Lindberg et al. 2002; Tsiafouli et al. 2005; Badejo and Akinwale 2006; Chikoski et al. 2006), however these studies were all conducted in forest habitats; an irrigation study carried out by Kardol et al. (2011) in an old-field ecosystem found no effects of moisture on mites. It may be that mite assemblages within grassland and desert systems are more resistant to drought stress than those within forested systems: within grassland and desert systems there tends to be little cover provided from the litter layer to fluctuations in ambient climatic conditions, which may favor assemblages that are more tolerant to a boom-and-bust moisture economy. The presence of a thicker litter layer within forests helps insulate the soil habitat from large swings in microclimatic conditions, and this may reduce the importance of drought resistance as a structuring factor on mite communities within these systems and may account for the stronger response of these communities to drought when the system is subjected to simulated extreme events.

***Implications for Ecosystem Functioning*** - Observed shifts in the proportional abundance of trophic groups within this study have implications for subsequent shifts in ecosystem functioning. Moore and Hunt (1988) noted that soil food webs could be sorted into three “energy channels” within two main categories: bacterial- and fungal-mediated channels fall within the detritus pathway and are contrasted to the root-derived pathway that takes energy directly from living plants through belowground herbivory. Within this study, we found the ratio of fungal-

feeding nematodes relative to bacterial-feeding nematodes to increase with increasing moisture availability both across the entire gradient and within KNZ; in contrast, this ratio decreased with increasing moisture availability at JRN and SGS. Increases in root-feeding nematodes were observed across the CEMG and within all sites as moisture availability increased (even at MCM, where no higher plants are found, proportional increases of algal feeders were observed with increasing moisture). Knapp et al. (2008) note that in arid systems, fewer (but larger) precipitation events may allow water to penetrate more deeply into the soil profile and result in greater retention of moisture in soil, which could lead to reduced influence of fungal pathways within drylands, whereas the opposite may be true for wetter systems such as KNZ that may suffer greater water stresses. Systems with greater flows through fungal channels lose less N to leaching, denitrification and N<sub>2</sub>O emissions (de Vries et al. 2006; de Vries et al. 2011) and can lead to increased soil aggregation and storage of total organic C and N (Wilson et al. 2009); thus, depending on how changes to precipitation alter water balances within soil, nutrient cycling could be impacted. Given the increase in root-feeding organisms with increasing moisture availability in this study, this may also result in greater rates of belowground herbivory within more arid systems. An important caveat to this is that the use of abundance as a sole metric is not necessarily indicative of function: Ferris (2010) notes that abundance data of nematodes fail to account for other life-history traits of these organisms, such as respiratory activity, duration of the life cycle or biomass, all of which can have important implications in a given individual's contribution to ecosystem functioning. Additionally, consideration of biomass as a response variable has been shown to potentially differ from analyses using abundance (Saint-Germain et al. 2007), which can have important implications in the study of trophic interactions and associated ecosystem functions (Brown et al. 2004).

## 4.6 Conclusions

This study represents one of the first to examine how alterations to a fundamental environmental control of the soil habitat such as soil water availability affect soil animals across a variety of ecosystems and at a larger regional/global scale, especially in a manner using similar methods across all sites to allow for true data comparisons (Petersen and Luxton 1982; Boag and Yeates 1998; Wall et al. 2008; Powers et al. 2009; Wu et al. 2011). Our findings suggest that changes to moisture regimes within the soil habitat will have important impacts on the structure of soil animal communities, both locally and regionally. As a consequence of alterations to precipitation regimes caused by climate change, xeric ecosystems are projected to see increases to available soil moisture while mesic ecosystems may see decreases (Knapp et al. 2008). Under these projections, our data suggest that soil nematode communities within xeric sites may see decreases to all trophic groups except for an increase in root-feeding nematodes (where present), increasing the amount of belowground herbivory within these systems. In contrast, mesic sites may see increases to all groups except for root-feeding nematodes, which will result in decreased root herbivory. Thus, while increases or decreases to moisture availability may have few serious effects on soil communities in the short term, over the longer-term climate change may influence species distributions and ecosystems regionally, especially given drought forecasts for the mid- and southwestern United States and arid lands globally which will punctuate the “new normal” of altered precipitation regimes with extreme drought events (Easterling et al. 2000; Strzepek et al. 2010). Above- and belowground systems may not respond in a similar manner or within synchronized timescales to climate change, and biome-scale responses to these changes are unlikely to be captured within single-site studies. Working at multiple sites and including

responses of both major components of terrestrial ecosystems may therefore increase the ability of experiments to predict future ecosystem dynamics.

**Table 4.1:** Climate and vegetation for sites used within this study. References for climate data are: KNZ, Hayden 1998; SGS, Lauenroth and Sala 1992; JRN, Hochstrasser et al. 2002; MCM, Doran et al. 2002.

Site	Coordinates	MAT (°C)	MAP (mm)	Dominant vegetation
KNZ	39.093N, -96.575W	13	835	Big bluestem ( <i>Andropogon gerardii</i> ; Vitman) Little bluestem ( <i>A. scoparius</i> ; (Michx.) Nash) Yellow indiagrass ( <i>Sorghastrum nutans</i> ; (L.) Nash)
SGS	40.827N, -104.724W	8.6	321	Blue grama ( <i>Bouteloua gracilis</i> ; (Willd. Ex. Kunth) Lag. Ex Griffiths)
JRN	32.618N, -106.740W	14.7	248	Black grama ( <i>Bouteloua eriopoda</i> ; Torr.) Honey mesquite ( <i>Prosopis glandulosa</i> ; Torr.) Creosote bush ( <i>Larrea tridentata</i> ; (DC.) Coville)
MCM	-77S, 162.52E	-19	< 100	Algae and cyanobacteria (soil surface) Mosses (along stream margins) Lichen (at higher elevation)

**Table 4.2:** Soil types and textures for the sites used in this study. Soils at KNZ are derived from limestone bedrock, those at SGS are derived from sedimentary bedrock, those at JRN from lacustrine and alluvial deposits and at MCM from glacial action with some lacustrine influence.

Site	Soil Type	% Sand	% Silt	% Clay	% Soil Moisture
Konza Prairie (KNZ)					
Summit	Cherty silt loam	20	52	28	12.01 – 45.72
Slope	Silty clay	18	40	42	18.97 – 45.00
Bottom	Silty clay loam	27	44	29	16.87 – 45.38
Addition/Ambient	Silty clay loam	5	60	35	15.06 – 51.75
Jornada Basin (JRN)					
Summit/Slope	Fine sandy loam	60	25	15	0.63 – 5.00
Bottom	Clay loam	35	32	33	2.71 – 8.31
Addition/Reduction/Ambient	Sandy loam/Loamy sand	77	15	8	0.66 – 12.03
Shortgrass Steppe (SGS)					
Summit/Slope	Gravelly sandy loam	75	10	15	1.62 – 13.79
Bottom	Fine sandy loam	60	30	10	2.35 – 15.00
Reduction/Ambient	Sandy loam	68	20	12	1.44 – 13.40
McMurdo Dry Valleys (MCM)					
Mean estimate	Sand	95	3	2	0.40 – 12.15



**Table 4.3:** Plot sizes and replicate numbers for treatments from existing precipitation manipulation experiments from each site used in this study. Additional information on individual experiments can be located in supplied references.

Site	Treatment	Plot Size (m)	# Replicates	Reference
KNZ	Ambient control	5 x 5	1	Knapp et al. 1994
	Addition	5 x 5	1	
SGS	Ambient control	2.5 x 2	6	Cherwin and Knapp 2012
	80% reduction	2.5 x 2	6	
JRN	Ambient control	2.5 x 2	6	Reichmann et al. 2013
	80% reduction	2.5 x 2	6	
	80% addition	2.5 x 2	6	
MCM	Ambient control	1 x 1	8	Simmons et al. 2009
	Addition	1x1	8	

**Table 4.4:** Nematode and mite trophic group percent composition by site. Percent composition represents mean values for all samples per site and so total percentages add up to  $100 \pm 0.01$ .

Site	Nematode Groups				Mite Groups		
	Bacterial-feeders	Fungal-feeders	Root-feeders	Omnivores	Predators	Generalists	Predators
JRN	69.95	0.88	19.53	8.87	0.78	88.33	11.67
KNZ	8.79	0.98	78.65	9.01	2.56	76.16	23.84
MCM	95.35	NA	NA	4.65	NA	NA	NA
SGS	48.96	1.35	36.81	11.86	1.01	71.84	28.16

**Table 4.5:** Soil animal groups, diversity indices and best-fit model explaining changes in total abundances within KNZ. Model abbreviations are as follows: SM = soil moisture, 2WK = precipitation (2 week total prior to sampling), YTD = precipitation (year-to-date at time of sampling), 2ANP = ANPP (two years prior to sampling). \*P < 0.05 and \*\*P < 0.001. When no multi-term model was significant, values for most significant single term alone are shown. Mite groups and fungal-feeding nematodes are omitted as no significant effects for these groups were observed.

Group	Model	R <sup>2</sup>	N
Total Nematodes	SM+ 2ANP	0.61 *	15
Bacterial-Feeding Nematodes	SM+ 2WK	0.79 **	12
Root-Feeding Nematodes	2ANP	0.43 *	15
Omnivorous Nematodes	SM	0.49 *	15
Predatory Nematodes	YTD	0.01 *	12
Shannon Diversity	2ANP	0.26 *	15
Species Evenness	2ANP	0.28 *	15

**Table 4.6:** Soil animal groups, diversity indices and best-fit model explaining changes in total abundances within SGS. Model abbreviations are as follows: SM = soil moisture, PPT = precipitation (current year total), 2WK = precipitation (2 week total prior to sampling), YTD = precipitation (year-to-date at time of sampling). \*P < 0.05, \*\*P < 0.001 and \*\*\*P < 0.0001. When no multi-term model was significant, values for most significant single term alone are shown. Mite groups are omitted as no significant effects for mites were observed.

Group	Model	R <sup>2</sup>	N
Total Nematodes	YTD	0.82 ***	12
Bacterial-Feeding Nematodes	PPT	0.55 *	12
Fungal-Feeding Nematodes	YTD	0.70 **	11
Root-Feeding Nematodes	PPT+2WK	0.86 ***	12
Omnivorous Nematodes	PPT	0.64 *	12
Predatory Nematodes	PPT	0.37 *	10
Shannon Diversity	YTD	0.34 *	12

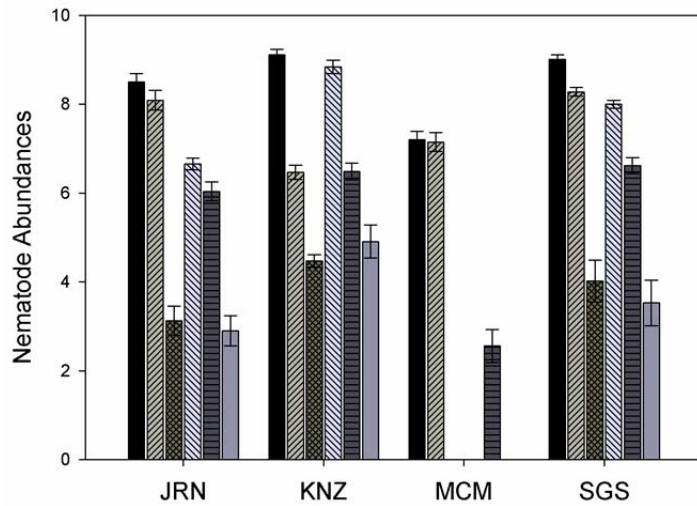
**Table 4.7:** Soil animal groups and best-fit model explaining changes in total abundances within MCM. Model abbreviation SM = soil moisture and \*P < 0.05. Only groups with significant effects are shown.

Group	Model	R <sup>2</sup>	N
Total Nematodes	SM	0.49 *	15
Bacterial-Feeding Nematodes	SM	0.51 *	15

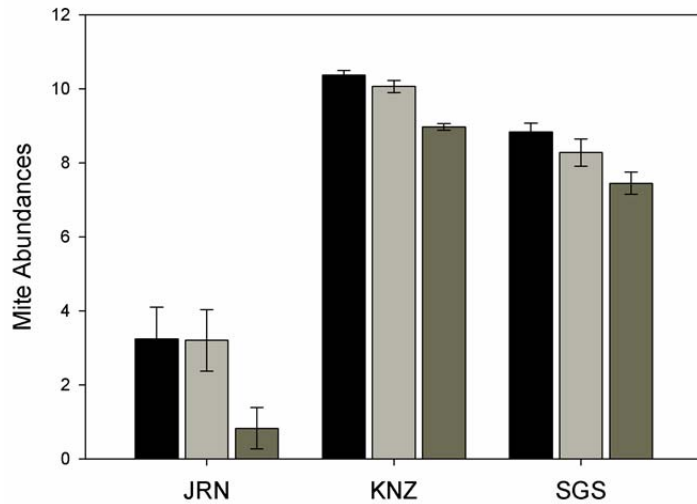
**Table 4.8:** Soil animal groups, diversity indices and best-fit model explaining changes in total abundances across the CEMG. Model abbreviations are as follows: SM = soil moisture, PPT = precipitation (current year total), 2WK = precipitation (2 week total prior to sampling), YTD = precipitation (year-to-date). \*\*P < 0.001 and \*\*\*P < 0.0001. When no multi-term model was significant, values for most significant single term alone are shown. Fungal-feeding nematodes are omitted as no significant effect for this group was observed.

Group	Model	R <sup>2</sup>	N
Total Nematodes	SM+PPT+SM*PPT	0.43 ***	37
Bacterial-Feeding Nematodes	SM	0.32 ***	63
Root-Feeding Nematodes	SM+PPT+SM*PPT	0.70 ***	36
Omnivorous Nematodes	SM+PPT+SM*PPT	0.38 **	37
Predatory Nematodes	ln (SM)	0.58 ***	42
Total Mites	YTD	0.52 **	20
Generalist Mites	ln (SM)	0.67 ***	27
Predatory Mites	ln (SM)+2WK	0.61 **	18
Shannon Diversity	2ANP	0.30 *	28
Species Evenness	2ANP	0.49 ***	28

a)

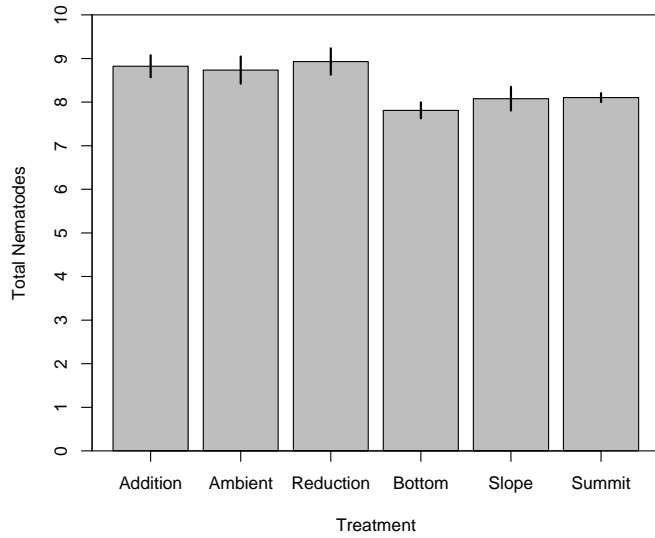


b)

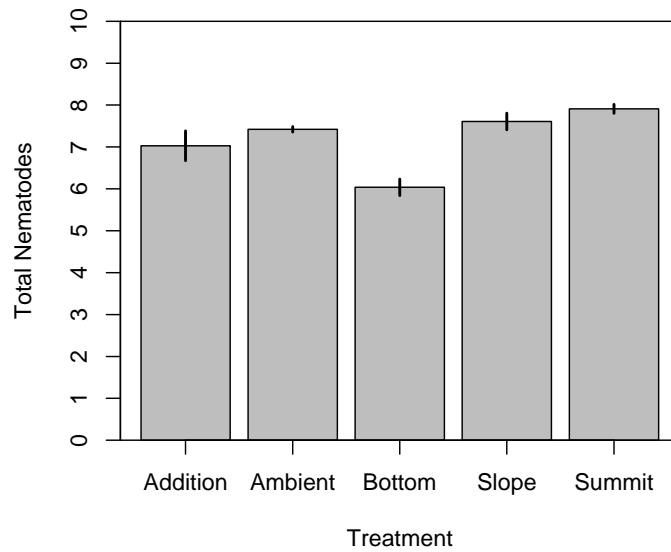


**Figure 4.1:** Mean abundances for soil animals from each site in this study a) total nematodes and nematode trophic groups: Total nematodes = black bar, bacterial-feeding nematodes = grey bar with left diagonal, fungal-feeding nematodes = grey bar with crosshatch, root-feeding nematodes = light grey bar with right diagonal, omnivorous nematodes = dark grey bar with horizontal lines and predatory nematodes = solid grey bar; and b) total mites and mite trophic groups: Total mites = black bar, generalist mites = light grey bar and predatory mites = dark grey bar. All abundance values are reported as  $\ln(x + 1)$ , with numbers of nematodes given as individuals  $\text{kg}^{-1}$  dry soil and numbers of mites given as individuals  $\text{m}^{-2}$  to a depth of 10 cm. Error bars represent standard errors.

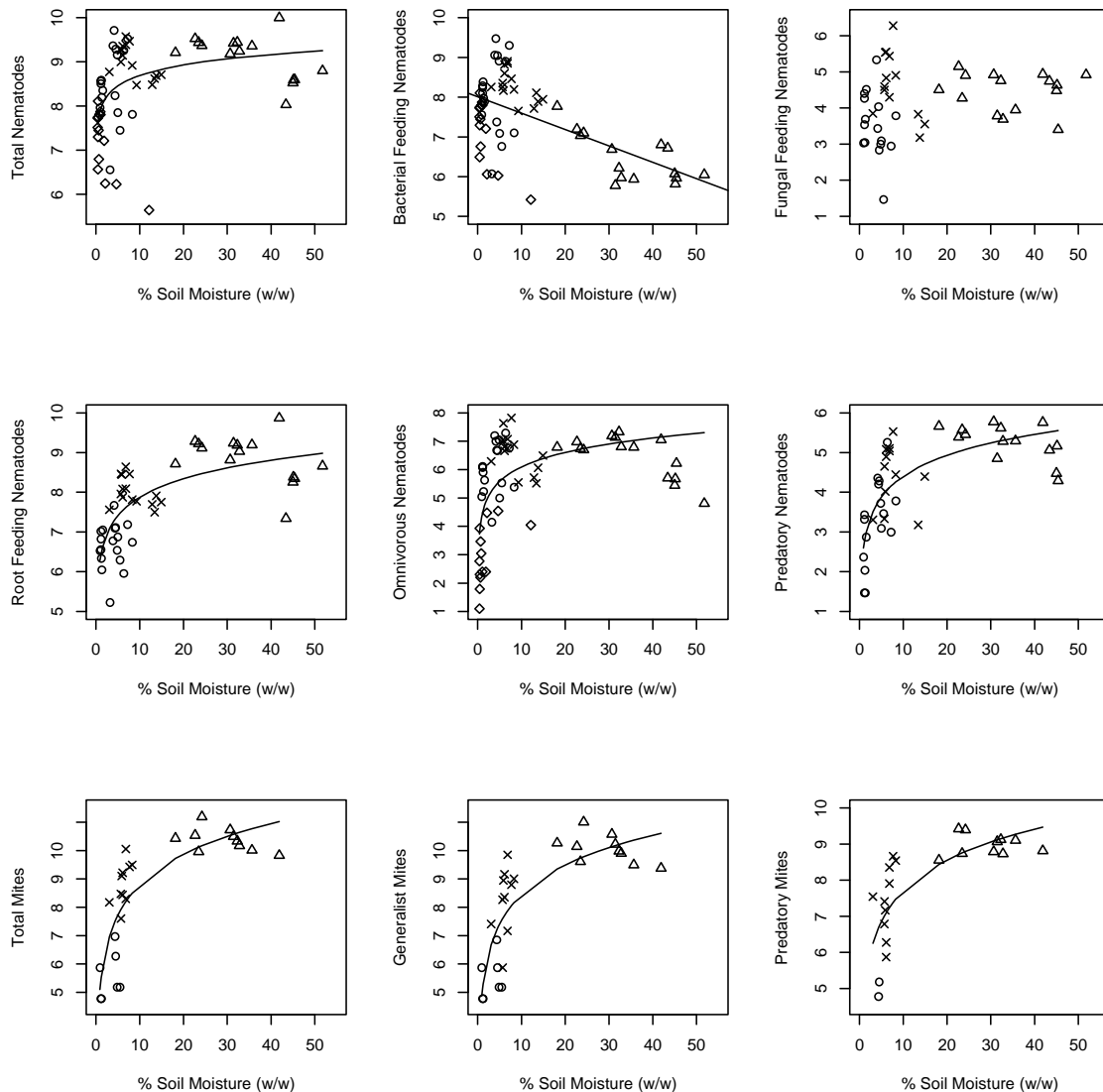
a)



b)

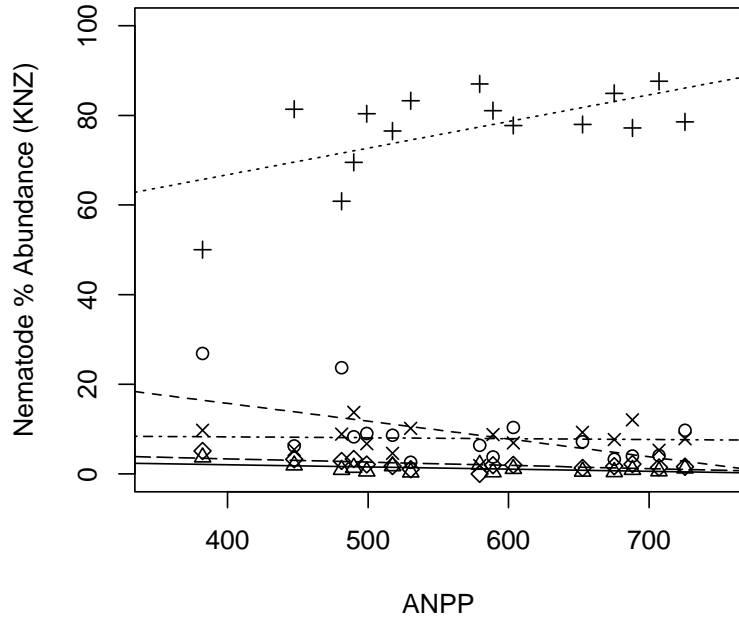


**Figure 4.2:** Response of nematode abundances (individuals  $\text{kg}^{-1}$  dry soil) to treatments within a) JRN ( $F_{5,36} = 3.59$ ,  $p = 0.01$ ) and b) MCM ( $F_{4,10} = 11.89$ ,  $p = 0.0008$ ). Abundance values shown as  $\ln(x + 1)$ , with numbers of nematodes given as individuals  $\text{kg}^{-1}$  dry soil, numbers of mites given as individuals  $\text{m}^{-2}$  to a depth of 10 cm. and error bars represent standard errors.

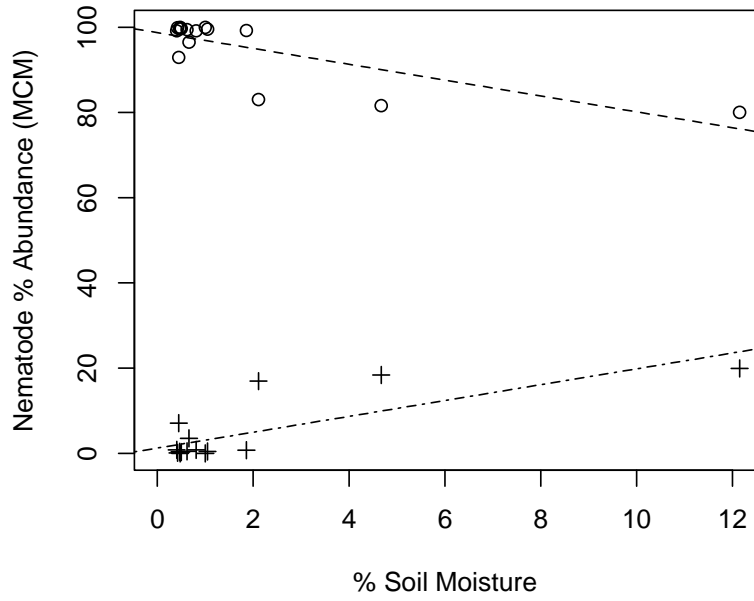


**Figure 4.3:** Changes in total abundances of mite and nematode groups and as a response to soil moisture across the overall gradient. All abundance values are reported as  $\ln(x + 1)$ , with numbers of nematodes given as individuals  $\text{kg}^{-1}$  dry soil and numbers of mites given as individuals  $\text{m}^{-2}$  to a depth of 10 cm. Symbols for each site are open circles for JRN, open triangles for KNZ, open diamonds for MCM and crosses for SGS. Total nematodes  $R^2 = 0.25^{***}$ ,  $n = 63$ ; bacterial-feeding nematodes  $R^2 = 0.32^{***}$ ,  $n = 63$ ; fungal-feeding nematodes  $R^2 = 0.04$ ,  $n = 44$ ; root-feeding nematodes  $R^2 = 0.54^{***}$ ,  $n = 48$ ; omnivorous nematodes  $R^2 = 0.40^{***}$ ,  $n = 61$ ; predatory nematodes  $R^2 = 0.58^{***}$ ,  $n = 42$ ; total mites  $R^2 = 0.69^{***}$ ,  $n = 27$ ; generalist mites  $R^2 = 0.67^{***}$ ,  $n = 27$ ; predatory mites  $R^2 = 0.57^{***}$ ,  $n = 22$ .  $^{***}P < 0.0001$ .

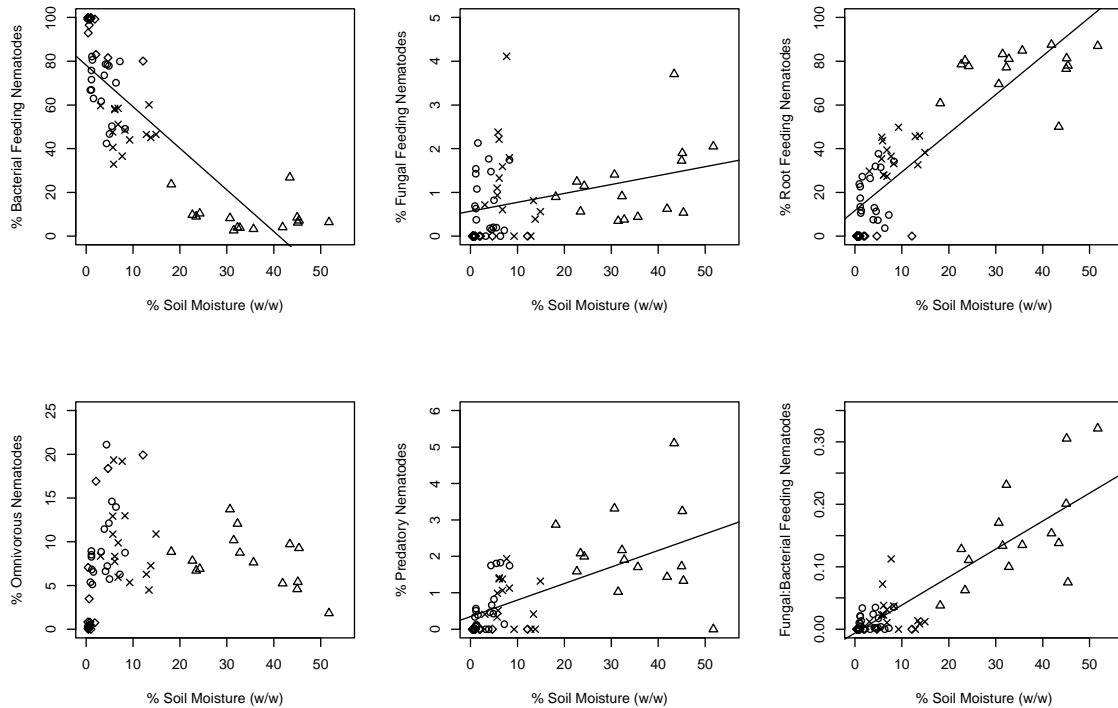
a)



b)



**Figure 4.4:** Changes in proportional distribution of nematode trophic groups as a response to environmental factors with the strongest effect on all trophic groups at a) KNZ and b) MCM. Note that for SGS no single factor was significant for all trophic group responses and at JRN only soil physical properties had a significant effect on proportional changes in trophic groups. For KNZ, % bacterial-feeders  $R^2 = 0.29^*$ ; % fungal-feeders  $R^2 = 0.28^*$ ; % root-feeders  $R^2 = 0.33^*$ ; % omnivores  $R^2 = -0.07$ ; % predators  $R^2 = 0.37^*$ . For MCM, % bacterial-feeders  $R^2 = 0.57^{**}$  and % omnivores  $R^2 = 0.57^{**}$ ; for all tests  $n = 15$  and only significant effects on trophic groups shown on graph. For regression lines and symbols, % bacterial-feeders = short dash line and open circles, % fungal-feeders = solid line and open triangles, % root-feeders = dotted line and plusses, % omnivores = dot-dash line and crosses and % predators = long dash line and open diamonds. \* $P < 0.05$ , \*\* $P < 0.001$  and \*\*\* $P < 0.0001$ .



**Figure 4.5:** Changes in proportional composition of nematode trophic groups and fungal:bacterial-feeding nematodes as a response to soil moisture across the overall gradient. Symbols for each site are open circles for JRN, open triangles for KNZ, open diamonds for MCM and crosses for SGS. % Bacterial-feeders  $R^2 = 0.70^{***}$ ; % fungal-feeders  $R^2 = 0.09^*$ ; % root-feeders  $R^2 = 0.74^{***}$ ; % omnivores  $R^2 = -0.01$ ; % predators  $R^2 = 0.38^{***}$ ; fungal:bacterial-feeders  $R^2 = 0.75^{***}$ ; for all tests  $n = 63$ . \* $P < 0.05$ , \*\* $P < 0.001$  and \*\*\* $P < 0.0001$ .



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## **5 Direct and indirect effects of soil moisture and trophic interactions on soil animal communities**

### **5.1 Summary**

Soil moisture has long been known to be an important factor for soil communities, both in providing habitat space for soil organisms as well as in controlling decomposition dynamics. Despite this importance, the direct and indirect effects of changes in moisture availability within soil communities are not well understood and it is unclear to what degree soil moisture is important in structuring communities of soil animals. To address this, we present a structural equation model investigating the role soil moisture and trophic interactions play in structuring communities of mites and nematodes. Soil cores were collected from hill-slope transects along a climate gradient of mesic, xeric and desert grasslands in the central and southwestern United States in 2010 and 2011. Soil moisture was determined at the time of sampling and mites and nematodes were extracted and sorted to trophic groups. Our results indicate soil moisture has a strong effect on soil animal trophic groups and that trophic effects within the community are mediated in a top-down fashion. Interestingly, these effects do not appear to be due to predation, but suggest the influence of environmental variables such as plant production, precipitation or soil texture that co-vary with moisture and animal abundances within our system but were not included in our analyses. These findings indicate that soil communities are strongly affected by abiotic environmental factors and also suggest that dynamics within soil animal communities are more complex than trophic linkages alone may imply.

## 5.2 Introduction

Soil moisture availability is an important environmental variable in terrestrial ecosystems: while precipitation (along with temperature and other climate factors) contributes to the outlining of biomes and species distributions at regional or greater scales (Chapin et al. 2011), the interplay of temperature, topography and soil physical characteristics with precipitation controls soil moisture availability (Kramer and Boyer 1995; Porporato et al. 2004). Soil moisture availability represents the immediate source of water for above- and belowground ecosystems, with losses to evaporation and transpiration replenished by precipitation events (Porporato et al. 2004). Soil moisture provides water for plant productivity aboveground, while belowground it controls many aspects of the soil system including soil chemistry, habitat space for soil organisms and plant rooting strategies (Kramer and Boyer 1995; Bardgett 2005).

Soil moisture availability is therefore an important factor in ecosystem functioning: plant productivity is the energy foundation for terrestrial ecosystems, and moisture and temperature have been identified as key variables in decomposition processes globally (Swift et al. 1979; Trofymow et al. 2002), rates of which may be further accelerated in some biomes by the presence of soil animals such as mites and nematodes (e.g. Wall et al. 2008; Powers et al. 2009). These two groups of organisms feature different life histories that result in alternative uses of the soil habitat: nematodes are aquatic organisms that live within the water film along the surface of soil particles and mites occupy the air-filled pores of the soil substrate, although both groups require some degree of moisture availability to carry out basic life functions (Coleman et al. 2004; Bardgett 2005). Mites and nematodes are both taxa where high numbers of described species are thought to represent only a small fraction of total species present within ecosystems (e.g. Walter et al. 1996; Bloemers et al. 1997; Brussaard et al. 1997; Lawton et al. 1998). As a



consequence of this high diversity, these two groups are also ecologically diverse, having a large variety of trophic roles ranging from primary consumers feeding upon root tissue, microbial and fungal grazers to predatory individuals feeding upon other mites and nematodes, which leads to numerous interactions and feedbacks between populations of each of these groups (Yeates et al. 1993; Walter and Proctor 1999).

The numerous species interactions resulting from this high diversity increase the difficulty in determining responses to experimental manipulations or changes in environmental conditions, especially when coupled with the microscopic size of soil organisms and the opaque nature of the soil habitat. Direct effects of environmental changes can be well captured through experimental manipulations such as studies on drought (Lindberg et al. 2002; Tsiafouli et al. 2005; Bakonyi et al. 2007; Landesman et al. 2011) and warming (Zhang et al. 2005; Simmons et al. 2009), however indirect effects within soil ecosystems have been best captured through simplified mesocosms (e.g. Ingham et al. 1985) or by conducting experiments in ecosystems with less complex communities (Wall and Virginia 1999). In order to identify indirect effects in more complex ecosystems such as forests and grasslands, experimental methods such as these are increasingly being complemented by the application of Structural Equation Modeling (SEM), a multivariate analytical technique that employs both path and factor analyses in order to investigate linkages (both direct and indirect) among variables (Grace 2006). Using experimental data, this approach has been used, for example, in ecological analyses to examine the influence of environmental variables on soil microbial communities (Allison et al. 2007), tease apart effects of multiple global change drivers on soil communities (Eisenhauer et al. 2012) and examine the role of soil food webs in nutrient losses (de Vries et al. 2012). As such, this

technique appears to provide a powerful analytical tool to disentangle complex ecological relationships.

We examined the effects of altered soil moisture regimes on communities of mites and nematodes along a large-scale climate gradient across three grassland types in the central and southwestern US (mesic, xeric and shrub-invaded desert grassland). We selected these locations to provide insight into the dynamics of soil community interactions and altered soil moisture regimes across grasslands and arid lands, which make up a large portion of the terrestrial surface of Earth (MEA 2005). Our objective was to examine the influence of changes in soil moisture and interactions between trophic groups in structuring soil animal communities, which we approached using SEMs. Our hypotheses took the form of two alternative conceptual models to be tested: our first model predicts (1) bottom-up controls where soil moisture influences bacterial-, fungal- and root-feeding trophic groups that in turn influence higher trophic levels within the soil food web (Figure 5.1a). We expect this to be the model best supported by the data as there is generally high resource availability within the sites of this study and the soil communities studied are unlikely to be resource limited. Our second model predicts (2) a system where the lowest-level trophic groups are influenced by soil moisture, but also influenced by higher trophic groups in a top-down manner (Figure 5.1b). Predatory organisms were generally found in low densities in samples within this study and so we expect the data will support this model less well as compared to hypothesis (1).

### **5.3 Materials and Methods**

We collected data for this study along a broad-scale precipitation gradient comprising three long-term ecological research (LTER) sites across the central and southwestern United

States. These three sites provided a gradient across grasslands and aridlands, and included remnant tallgrass prairie near Manhattan, KS (KNZ, mesic grassland; 39.093N, -96.575W), shortgrass prairie near Fort Collins, Colorado (SGS, xeric grassland; 40.872N, -104.724W) and shrub-invaded desert grassland near Las Cruces, New Mexico (JRN, arid grassland; 32.618N, -106.740W). Within each site a soil moisture gradient was created by establishing three 5 x 5 m plots along a hill-slope transect with one plot at the summit, one along the slope and one at the base of the slope. Additionally, ambient treatments from pre-existing experiments manipulating precipitation were sampled in order to include additional data points for model construction.

***Sampling Protocol*** - Soil sampling was carried out twice in 2010 and three times in 2011, with samples collected in the summer and fall of 2010 and late spring, midsummer and fall of 2011, which corresponded to before, during and after the wet season at each site. At the time of sampling, separate soil cores were collected for mites and nematodes because of the different extraction methods used for isolating each taxon from the soil substrate. For nematodes, soil cores measuring 10 cm deep and 2.5 cm in diameter were collected and for mites soil cores measured 10 cm deep and 6 cm in diameter; the larger diameter core for mites facilitated extraction by minimizing compression along the edges of the core relative to the overall volume of the core.

While single cores were used for mite extractions, bulk soil samples were collected for nematodes by aggregating eight soil cores from each plot or treatment type: eight soil cores were collected at random from within each 5 x 5 m plot along the hill-slope gradients and from the experimental manipulations at KNZ while single cores were collected from random locations from within each plot of the experimental manipulations at JRN, SGS and KNZ. All samples were stored in coolers and returned to the laboratory where the bulked soils were subsampled for

gravimetric soil moisture analyses (50 g) and nematode extractions (100 g). Mites were extracted from single cores taken randomly from within each 5 x 5 m plot along the hill-slope gradients within each site and from within a randomly selected replicate plot for the experimental manipulations, and these cores were not subsampled prior to extraction. For additional environmental data and collection methods, see chapter 4 of this dissertation.

***Extraction and Identification*** - Mites and nematodes were extracted using different techniques. Mites were extracted using modified Tullgren funnels (Crossley and Blair, 1991) with a heat gradient applied over 7 days. Cores were split in half by depth to increase extraction efficiency and specimens were collected and stored in 70% ethanol. Once extracted, mites were counted and sorted to predatory (mesostigmatid) and generalist microbial/detrital grazing (oribatid and prostigmatid) trophic groups (Walter and Proctor 1999). Nematodes were extracted using a modified sugar centrifugation-floatation method (Freckman and Virginia 1993) and counted and sorted to trophic groups while live (see Yeates et al. 1993) before being preserved in 5% formalin solution. Mites and nematodes were sorted to trophic groups in order to compare ecological commonalities in the soil community across sites. Nematodes were counted using an Olympus CKX41 inverted microscope at 100-400X and mites were counted using a SZX9 dissecting microscope.

***Data Analysis*** - We used a structural equation modeling (SEM) technique to investigate the relationships between soil moisture availability and soil animal trophic groups across a regional precipitation gradient. SEM analysis employs a multivariate approach to data involving path and factor analyses, facilitating the comparison of hypothetical models with experimental data in order to identify direct and indirect relationships between environmental and community factors (Grace 2006). Path coefficients are calculated for each set of connected variables within

the model, representing the effects on the dependent variable of a change of a one standard deviation alteration in the independent variable if all other variables are held constant (Mitchell 1992). Resulting models can then be compared for goodness-of-fit using the  $\chi^2$  statistic, with a significant ( $p \leq 0.05$ ) value indicating rejection of the null hypothesis that the proposed model matches the data and with non-significant p-values suggesting adequate fit between the data and the proposed model (Mitchell 1992).

Using existing models of trophic web interactions (e.g. Hunt et al. 1987; Wall and Virginia 1999) and previous analyses (chapter 4, this dissertation) as a guide, we constructed two SEM models to examine community dynamics within our data using a bottom-up (lower trophic groups influence abundance of higher trophic groups) and a top-down (higher trophic groups influence abundance of lower trophic groups) approach. The final model was constructed iteratively by adapting model parameters of best-fit models until a model with good fit and a solid mechanistic basis was identified. This model was run to examine the influence of soil moisture and trophic interactions across the soil moisture gradient encompassing all three sites.

Counts from all samples were standardized to numbers per square meter (mites) and numbers per kilogram dry soil (nematodes) prior to analyses in order to facilitate comparisons across samples and sites and natural-log transformed to meet assumptions of normality. All analyses were performed in R version 2.15.3 (R core team 2013), with SEM analysis using the lavaan package (Rosseel 2012).

## **5.4 Results**

The first proposed model (Figure 5.1a) did not provide a good fit to the data for the influence of soil moisture and trophic groups in structuring soil animal communities, however

the second proposed model (Figure 5.1b) did fit the data, albeit weakly ( $\chi^2 = 5.649$ ,  $df = 2$ ,  $p = 0.059$ ). We therefore used this second model as the basis for our iterative process to find a final model (Figure 5.2) that better fit the data ( $\chi^2 = 7.851$ ,  $df = 6$ ,  $p = 0.249$ ) by altering connections to the fungal-feeding nematode trophic group and removing a linkage between predators from both taxa. Among the lower nematode trophic groups soil moisture and both nematode and mite predators affected root-feeding nematodes, while bacterial-feeding nematodes were affected by soil moisture alone; fungal-feeding nematodes showed no significant interactions with any variables used. For higher nematode trophic groups, predators were affected by soil moisture and omnivorous nematodes were affected by predatory nematodes alone. Amongst mite trophic groups, predatory mites were affected by soil moisture and both soil moisture and predatory mites affected generalist mites. Strengths of the direct effects are summarized in Table 5.1. The indirect effect of soil moisture on omnivorous nematodes mediated through the effect of predatory nematodes ( $0.224 = 0.56 \times 0.40$ ) was nearly twice that of the (non-significant) direct effect (0.14). The final fitted model also explained a large portion of the variation for most trophic groups: 79% for root-feeding nematodes, 71% for generalist mites, 61% for predatory mites, 43% for omnivorous nematodes, 34% for bacterial-feeding nematodes, and 31% for predatory nematodes but only 8% for fungal-feeding nematodes.

## 5.5 Discussion

The results of our SEM analysis support the importance of soil moisture availability in structuring communities of soil animals, as soil moisture was the strongest single influencing variable found within our final model for nearly all groups, with the exception of fungal-feeding nematodes and omnivorous nematodes. Nematodes are highly dependent upon moisture availability to carry out life processes (Coleman et al. 2004; Bardgett 2005) and when available

soil moisture decreases beyond a critical threshold these organisms enter anhydrobiosis (a state of extremely low metabolic activity) until moisture availability increases to a suitable level (Treonis et al. 2000; Adhikari et al. 2009). Despite their habitation of air-filled soil pores, mites also require a degree of soil moisture in order to avoid desiccation (Walter and Proctor 1999) and commonly employed extraction methods utilize heat gradients along soil cores (e.g. Crossley and Blair 1991). Additionally, studies on the effects of changes to soil moisture on soil animal communities within single ecosystems have shown changes to mite and nematode community composition (Yeates and Bongers 1999; Lindberg et al. 2002; Tsiafouli et al. 2005; Nielsen et al. 2012).

The strength and directionality of the responses for trophic groups from sites used within this study are largely in agreement with those within our earlier study (Chapter 4), with the exception of omnivorous nematodes. In our previous study, this group of soil animals demonstrated a significant increase as soil moisture availability increased, however such a relationship is not seen within our SEM analysis. This is most likely due to the omission of data from the McMurdo Dry Valleys LTER site used in our prior study, where omnivorous nematodes showed a sharp (though not significant) increase with moisture availability (Chapter 4) but which could not be used in these analyses because of the lack of several trophic groups included within our models for this study. Within MCM, omnivorous nematodes have been observed to increase in abundance with increased soil moisture (Treonis et al. 1999; Courtright et al. 2001), and so omitting this data from our SEM analysis may be responsible for the altered response strength reported by our final model as compared to our prior findings (Chapter 4).

Our final model (Figure 5.2) demonstrates top-down effects of predatory mites and nematodes on lower trophic groups, however these effects do not appear to be due to predation.

Path coefficients within the model represent the effect of a one standard deviation change in the independent variable upon the dependent variable (Mitchell 1992) and so a predatory response would be expected to be negative in directionality. However the path coefficients in our model indicate a positive relationship that is not consistent with the interpretation of predation and suggest that the predatory trophic groups may be acting as indicators of the influence of environmental variables that were not included in this analysis such as precipitation, plant productivity and soil texture and that co-vary with variables measured within this study.

The poor model fit of our first proposed model (Figure 5.1a) had hypothesized effects of environmental variables within our system would be mediated by lower trophic levels within the soil community, yet it appears as though the impact of any additional co-varying environmental factors is expressed through the system in a top-down manner by the predatory trophic groups. There are several likely candidate environmental variables that may influence soil communities and help explain this response, including precipitation (e.g. Irmeler 2006; Nielsen et al. 2010), plant species identity, diversity or productivity (e.g. Hansen and Coleman 1998; Porazinska et al. 2003; Sylvain and Buddle 2010; Eisenhauer et al. 2012) and soil texture (e.g. Jones et al. 1969; Yeates and Bongers 1999), although it is unclear why these factors would be observed acting indirectly through predatory groups. The positive relationship of predatory mites on generalist mites may indicate changes in habitat suitability for mites in general and therefore have no bearing on predation. Similarly, the effects of predators on nematodes within lower trophic levels may reflect the movement of predatory organisms throughout the soil profile in response to changing habitat conditions, which could indicate the positive relationships observed within our final model reflect changes in habitat suitability for organisms within lower trophic levels; McBrayer et al. (1977) reported vertical movement of some microarthropod groups in response



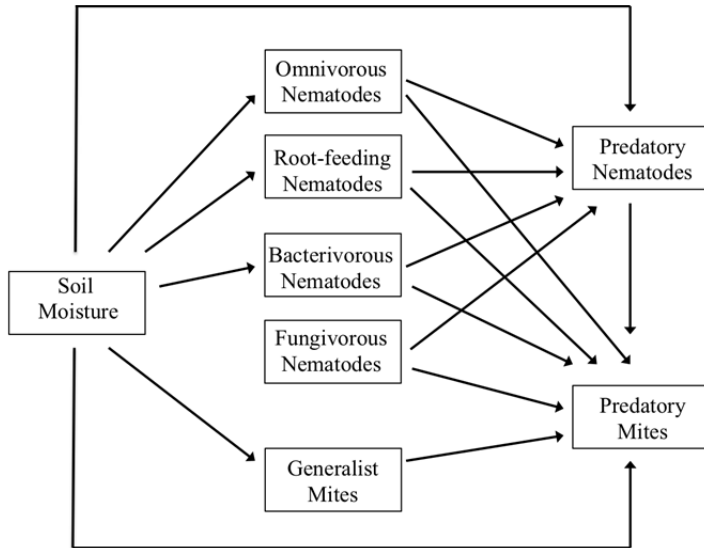
to temperature changes, and this pattern may be observed due to changes in soil moisture availability within our study. While our prior study (Chapter 4) examined the effects of precipitation, annual net primary production and soil texture on communities of soil animals, these factors were not included within our SEM analysis; variances within these variables were much lower than the variances for gravimetric soil moisture and trophic group abundances due to how these variables were measured, and initial models constructed in these analyses appeared to be sensitive to large differences in the variances of model variables. An additional consideration for the observed trophic interactions within this study is that analyses are based upon abundance data: some authors have suggested that abundance data may not be the best metric in order to capture certain ecological phenomena, with response variables including biomass as a more accurate estimator in some cases (Saint-Germain et al. 2007; Ferris 2010).

We have shown that soil animal communities strongly respond to changes in soil moisture availability and that additional factors within ecosystems may influence soil communities through top-down effects from predatory trophic groups on the remainder of the soil animal community. This study suggests that by employing a sampling protocol inclusive of the requirements of SEM analysis it should be possible to better tease apart the effects of higher trophic groups and identify other factors having strong effects on the soil community. With a better understanding of the factors that influence soil animal communities and the strength and directionality of responses of soil animals to changes in these factors, we can develop a clearer picture of how these communities may respond to climate and land-use change. Given that the ecosystems similar to those used in this study comprise a large portion of the terrestrial surface of the planet, understanding these changes will allow us to plan for shifts to soil ecosystem functioning that have large effects globally.

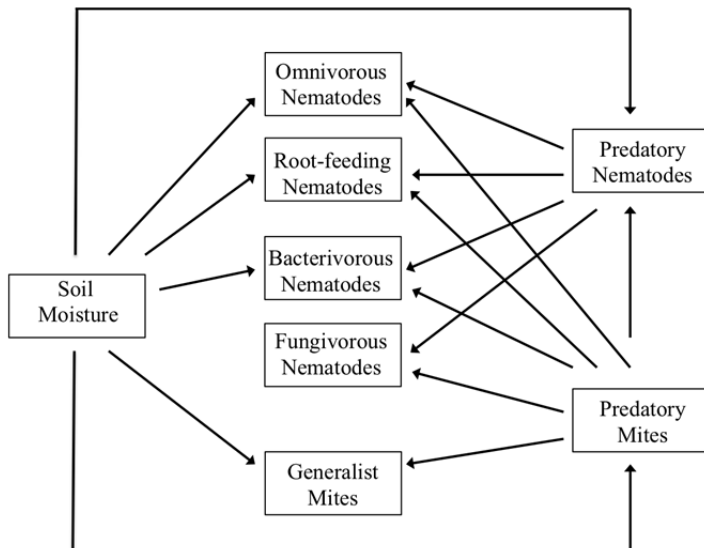
**Table 5.1:** Coefficient estimates and standard errors for significant relationships between soil moisture and trophic groups in final SEM. For Z-values, significance level is denoted as  $p < 0.05 = *$ ,  $p < 0.01 = **$  and  $p < 0.001 = ***$ .

Dependent variable	Independent variable	Estimate $\pm$ SE	Z-value
Predatory nematodes	% Soil moisture	1.08 $\pm$ 0.19	5.80***
Predatory mites	% Soil moisture	3.13 $\pm$ 0.21	14.64***
Omnivorous nematodes	Predatory nematodes	0.15 $\pm$ 0.06	2.41*
Root-feeding nematodes	% Soil moisture	0.42 $\pm$ 0.12	3.67***
	Predatory nematodes	0.10 $\pm$ 0.03	3.19**
	Predatory mites	0.10 $\pm$ 0.03	3.52***
Bacterial-feeding nematodes	% Soil moisture	-0.76 $\pm$ 0.20	-3.71***
Generalist mites	% Soil moisture	1.81 $\pm$ 0.54	3.35**
	Predatory mites	0.43 $\pm$ 0.15	2.91**

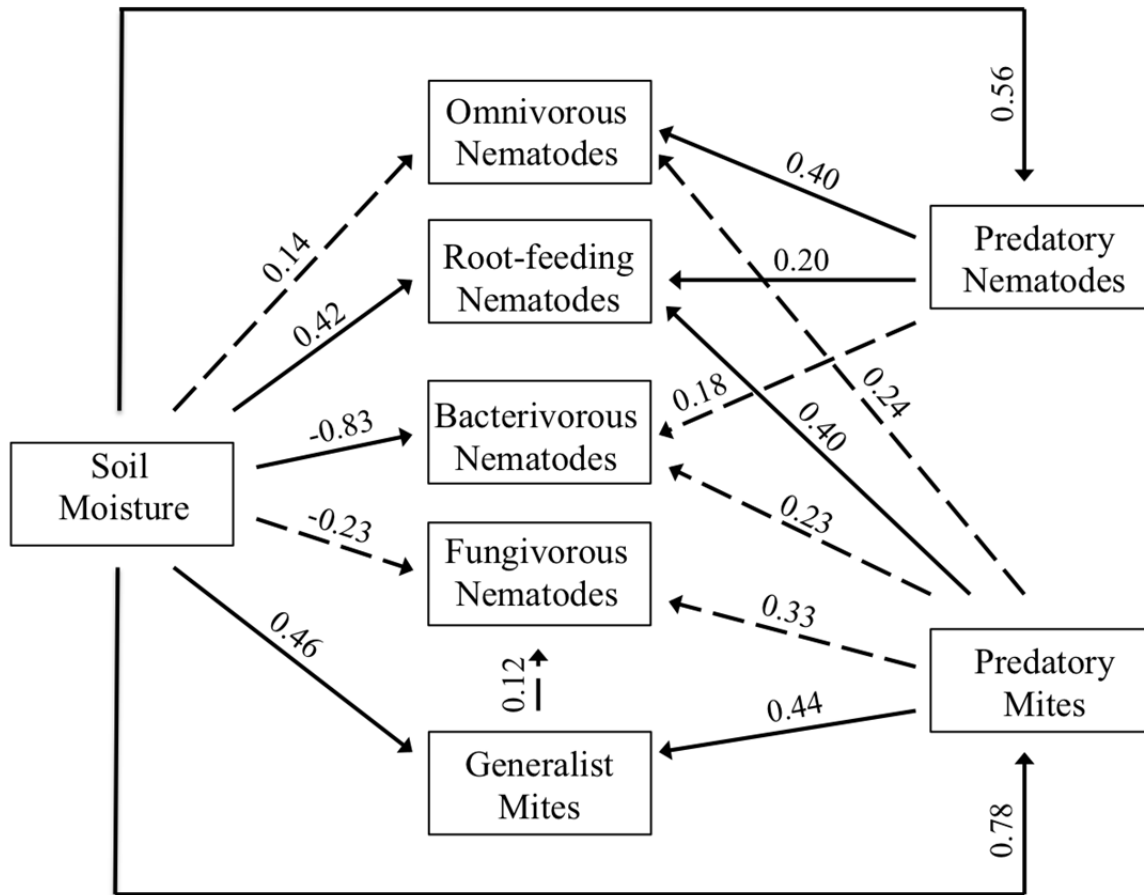
a)



b)



**Figure 5.1:** Proposed conceptual models hypothesizing either a) a bottom-up model for soil animal community interactions with soil moisture availability and trophic interactions mediated by lower-level trophic groups on higher-level groups or b) a top-down model for soil animal communities with effects of soil moisture availability on soil animals at all levels and trophic interactions from higher-level trophic groups on lower-level groups.



**Figure 5.2:** Final fitted model used to estimate strength of direct and indirect effects of soil moisture and trophic interactions in the soil animal community. Solid lines indicate significant ( $p < 0.05$ ) interactions and dashed lines indicate non-significant interactions, with values for estimates of standardized path coefficients.

## 5.6 References

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