

Soil animal responses to moisture availability are largely scale, not ecosystem dependent: insight from a cross-site study

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Abstract

Climate change will result in reduced soil water availability in much of the world either due to changes in precipitation or increased temperature and evapotranspiration. How communities of mites and nematodes may respond to changes in moisture availability is not well known, yet these organisms play important roles in decomposition and nutrient cycling processes. We determined how communities of these organisms respond to changes in moisture availability and whether common patterns occur along fine-scale gradients of soil moisture within four individual ecosystem types (mesic, xeric and arid grasslands and a polar desert) located in the western United States and Antarctica, as well as across a cross-ecosystem moisture gradient (CEMG) of all four ecosystems considered together. An elevation transect of three sampling plots was monitored within each ecosystem and soil samples were collected from these plots and from existing experimental precipitation manipulations within each ecosystem once in fall of 2009 and three times each in 2010 and 2011. Mites and nematodes were 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 CEMG, within individual ecosystems, increases in soil moisture resulted in decreases to nematode communities at all but the arid grassland ecosystem; mites showed no responses at any ecosystem. In addition, we found changes in proportional abundances of mite and nematode trophic groups as soil moisture increased within individual ecosystems, which may result in shifts within soil food webs with important consequences for ecosystem functioning. We suggest that communities of soil animals at local scales may respond predictably to changes in moisture availability regardless of ecosystem type but that additional factors, such as climate variability, vegetation composition, and soil properties may influence this relationship over larger scales.

Keywords: climate change, desert, drought, grassland, mites, nematodes

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Introduction

Water availability is a major determinant of soil animal community composition and functioning, and climate change induced alterations of soil water content can 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) is an important driver of decomposition rates globally (Swift *et al.*, 1979; Moorhead *et al.*, 1999; Trofymow *et al.*, 2002). Soil animal communities can be

influenced by shifts in precipitation regimes, resulting in potential alteration of decomposition rates (Wall *et al.*, 2008; Blankinship *et al.*, 2011; Eisenhauer *et al.*, 2012) due to both physiological requirements and possibly as a result of moisture-related influences on vegetation communities and their productivity.

Soil animal communities are biologically and ecologically diverse (e.g. Yeates *et al.*, 1993; Walter *et al.*, 1996; Bloemers *et al.*, 1997; Walter & Proctor, 1999), and include numerous groups of organisms such as mites and nematodes, which use 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 and are physiologically active only when

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water is available (Coleman *et al.*, 2004; Bardgett, 2005). Responses of mites and nematodes to changes in precipitation and soil moisture availability are unclear and it is unlikely that taxa, or the trophic groups to which they can be assigned will respond in similar ways. Soil food webs can be separated into three 'energy channels': bacterial- and fungal-mediated channels comprise the detrital pathway, whereas root herbivores (pests, parasites, and pathogens) comprise the herbivory channel, which takes energy (carbon and nutrients) directly from living plant tissues (Moore & Hunt, 1988). Bacterial and fungal energy channels transfer carbon and nutrients through the detrital food web with varying efficiency: bacterial channels have greater losses of N to leaching, denitrification and N₂O emissions (de Vries *et al.*, 2006, 2011), while fungal channels tend to have increased soil aggregation and storage of total organic C and N (Wilson *et al.*, 2009). Changes in soil moisture availability may alter trophic patterns within soil communities and subsequently, alter ecosystem functioning.

The majority of studies examining soil animals have been conducted within a single biome and interstudy comparisons are problematic owing to differing methods in sample collection, isolation of animals, and method of identification (but see Heneghan *et al.*, 1999; Gonzalez & Seastedt, 2000; Wall *et al.*, 2008 and Wu *et al.*, 2011). Single-site studies provide useful information on the response of soil communities at the landscape level to climate change drivers (e.g. Tsiafouli *et al.*, 2005; Bakonyi *et al.*, 2007; Landesman *et al.*, 2011; Eisenhauer *et al.*, 2012), however comparisons across sites allow for the determination of more general patterns. For example, 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). Comparing multiple biome types often leads to commonalities in the response to drought (Huxman *et al.*, 2004), but few studies have compared multiple ecosystem types to reveal general patterns in the vulnerability of soil animal communities to climate change.

We investigated the effects of altered precipitation regimes on soil animals both within single ecosystems as well as across multiple ecosystem types. We examined the effects of changes in soil moisture on mite and nematode communities along a cross-ecosystem moisture gradient (CEMG) across three grassland ecosystems in the central and southwestern United States and in an extremely arid polar desert system in Antarctica; all ecosystems were part of the long-term ecological research (LTER) program operated by the National Science Foundation. The three grasslands included a mesic

grassland (Konza Prairie, KNZ), a xeric grassland (Shortgrass Steppe, SGS), and a hot desert (arid, shrub-invaded grassland; Jornada Basin, JRN) to provide a gradient across arid lands and grasslands, which comprise 41% of terrestrial ecosystems (Millennium Ecosystem Assessment, 2005). The Antarctic ecosystem (McMurdo Dry Valleys, MCM) provided both a location of extreme aridity as well as a polar desert comparison to the hot desert ecosystem. The objective of this research was to determine whether soil animal communities respond to changes in soil moisture regimes in a consistent manner both across and within the four studied ecosystems. This was accomplished by using natural moisture gradients (occurring across and within ecosystems) as well as experimental precipitation manipulations within each ecosystem.

We hypothesized that (1) increased water availability would increase soil animal abundances and alter community trophic structure along the CEMG and within the drier temperate ecosystems (JRN and SGS) while abundances within the polar desert (MCM) would decrease and patterns along the mesic ecosystem (KNZ) would show no change. We expected that moisture-limited ecosystems such as the semi-arid grassland (SGS) and hot desert (JRN) 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 ecosystem (KNZ) 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 and animal activity. In the polar desert ecosystem (MCM), the dominant soil nematode (*Scottinema lindsayae*) is highly specialized for arid habitats and has been observed to decrease as soil moisture availability increases (e.g. Treonis *et al.*, 1999), and so we expected this to be mirrored in overall abundance patterns there. We also hypothesized that (2) nematodes would respond more strongly than mites to changes in soil moisture availability. Nematodes are aquatic organisms intimately tied to soil moisture availability to facilitate activity, while mites can move throughout the soil habitat to access moister microhabitats. Finally we hypothesized that (3) animals at higher trophic levels would 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 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.

Materials and methods

Site descriptions

Research was carried out along a broad-scale precipitation gradient encompassing four ecosystems represented by LTER sites across the western United States and Antarctica. The four ecosystems ranged from wet to dry: three in the United States—Konza Prairie (KNZ), a mesic remnant tallgrass prairie near Manhattan, KS; Shortgrass Steppe (SGS), a xeric shortgrass prairie located northeast of Fort Collins, CO, USA; and Jornada Basin (JRN), a desert grassland north of Las Cruces, NM, USA; and a polar desert 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 1, with soil information in Table 2.

Experimental design

Within each of the four ecosystems, a soil moisture gradient across an elevation transect was monitored to provide a natural range of variation at the landscape scale. Three 5 × 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 the exception of MCM), with samples being taken from under plant cover and through the litter layer whenever possible. Sampling from bare ground was minimized except within MCM, where no vegetation cover is present.

In addition to the landscape-scale gradient of soil moisture within each ecosystem, existing experimental manipulations of moisture (generally an addition or reduction as a % of ambient precipitation) within each ecosystem were also used and allowed inclusion of extreme soil moisture values to determine how soil animals responded to conditions beyond normal limits. These pre-established plots varied in size and water manipulation treatments (Table 3). This design allowed us to study patterns both within individual ecosystem types as well as across the CEMG using both experimental and natural gradient methods.

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 h at 105 °C (Barrett *et al.*, 2008). Climate-related variables included annual precipitation from both the current and previous year, precipitation from both 2 weeks prior and over the current year prior to sampling, and aboveground net primary production (ANPP) for the current year, previous year and from 2 years prior, which were derived from data sets available on each LTER's web page (except MCM, where primary production and precipitation data were not available, the latter unavailable due to malfunctioning sensors). 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 (Soil Survey Staff) for JRN.

Sampling methods

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

Table 1 Climate and vegetation for sites used within this study. References for climate data are: Konza Prairie, Hayden (1998); Shortgrass Steppe, Lauenroth & Sala (1992); Jornada Basin, Hochstrasser *et al.* (2002); McMurdo Dry Valleys, Doran *et al.* (2002)

Site	Coordinates	MAT (°C)	MAP (mm)	Dominant vegetation
Konza Prairie	39.093N, -96.575W	13.0	835	Big bluestem (<i>Andropogon gerardii</i> ; Vitman) Little bluestem (<i>A. scoparius</i> ; (Michx.) Nash) Yellow indiagrass (<i>Sorghastrum nutans</i> ; (L.) Nash)
Shortgrass Steppe	40.827N, -104.724W	8.6	321	Blue grama (<i>Bouteloua gracilis</i> ; (Willd. Ex. Kunth) Lag. Ex Griffiths)
Jornada Basin	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)
McMurdo dry valleys	-77S, 162.52E	-19.0	<100	Algae and cyanobacteria (soil surface) Mosses (along stream margins) Lichen (at higher elevation)

Table 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. Soil moisture ranges reflect values determined gravimetrically from each site

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 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. For SGS, JRN and MCM, soil cores from treatment replicates were combined into a single bulk sample used for nematode extractions and soil moisture determination and a single mite core was collected randomly from one replicate per sampling period

Site	Treatment	Plot size (m)	No. of replicates	Reference
KNZ	Ambient control	5 × 5	1	Knapp <i>et al.</i> (1994)
	Addition	5 × 5	1	
SGS	Ambient control	2.5 × 2	6	Cherwin & Knapp (2012)
	80% reduction	2.5 × 2	6	
JRN	Ambient control	2.5 × 2	6	Reichmann <i>et al.</i> (2013)
	80% reduction	2.5 × 2	6	
	80% addition	2.5 × 2	6	
MCM	Ambient control	1 × 1	8	Simmons <i>et al.</i> (2009)
	Addition	1 × 1	8	

the wet season at each location. Sampling in Antarctica was limited by logistics and length of the research season; it was conducted once annually for 3 years (2009, 2010, 2011) in the middle of austral summer. Samples for mites were collected from the final five sampling periods for the US ecosystems. 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 ecosystems. 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, a single bulk sample for each treatment was created by aggregating samples taken from 5 × 5 m plots along the elevation gradients within each ecosystem or from the smaller plots used for experimental precipitation manipulations at each sampling period. Eight soil cores were taken randomly from within each of the 5 × 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 × 5 m plot for the elevation gradient within each ecosystem 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 & 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 & 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 organisms (mesostigmatid and some prostigmatid mites) or generalists feeding on fungi, bacteria or detritus with some opportunistic predators (oribatid and some prostigmatid mites; Walter & Proctor, 1999) and preserved in 70% ethanol; mite trophic groupings are less clear than those for nematodes as the limited data available are on a per-species basis, a level of resolution that was not practical for this study (but see Maraun *et al.*, 2011).

Nematode trophic groups and mite suborders were used to compare commonalities in composition and ecosystem roles across ecosystems. 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 ecosystem (excepting MCM, where mites are not present and transformation of nematode numbers is not necessary for comparisons): 1.4 g cm^{-3} (JRN; Monger, 2006 and SGS; Heisler-White *et al.*, 2009) and 1.5 g cm^{-3} (KNZ; Heisler-White *et al.*, 2009).

Statistical analyses

For all analyses, mites and nematodes were treated separately and data from the experimental manipulations and natural ecosystem gradients were analyzed together for each site and across the CEMG unless otherwise noted. Linear 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. In addition, analyses were conducted only on presence data (i.e. analyses excluded animal counts of 0) to examine the role moisture availability plays in controlling represented animal populations only; 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; diversity was calculated using the Shannon diversity index (H') and evenness was calculated as H'/H'_{\max} . 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 Core Development Team, 2010) with regressions conducted using the `lm` function of the default R package.

Results

Within-ecosystem and cross-ecosystem (CEMG) comparisons

Nematode numbers aggregated from all plots (both experimental and along the landscape-scale gradients) were generally high within all ecosystems, although the dominant groups differed between ecosystems (Fig. 1a, Table 4) and numbers of mites differed within each ecosystem where they were present, with generalist mites always more abundant than predatory mites (Fig. 1b, Table 4). The established precipitation manipulation 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

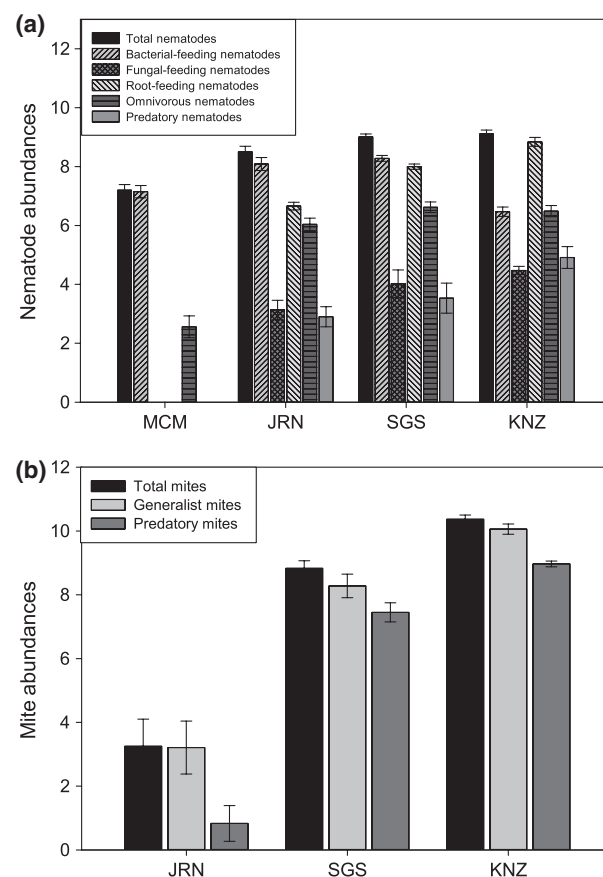


Fig. 1 Mean abundances for soil animals from each site in this study (a) total nematodes and nematode trophic groups and (b) total mites and mite trophic groups. All abundance values are reported as $\ln(x + 1)$, with numbers of nematodes given as individuals kg^{-1} dry soil and numbers of mites given as individuals m^{-2} to a depth of 10 cm. Error bars represent standard errors.

Table 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 ± 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

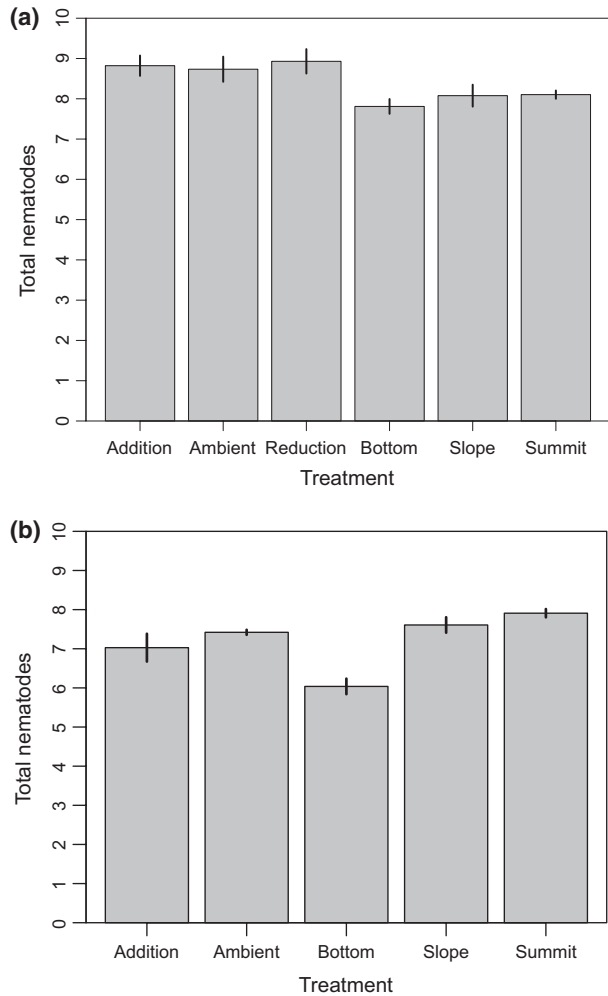


Fig. 2 Response of nematode abundances (individuals kg^{-1} dry soil) to treatments within (a) JRN ($F_{5,36} = 3.59, P = 0.01$) and (b) MCM ($F_{4,10} = 11.89, P = 0.0008$). Abundance values shown as $\ln(x + 1)$ and error bars represent standard errors.

gradient along the elevation transect (Fig. 2a), while effects within MCM mirrored expected trends in soil moisture (Fig. 2b).

Mites and nematodes responded to moisture in different ways. Numbers of nematodes from all trophic

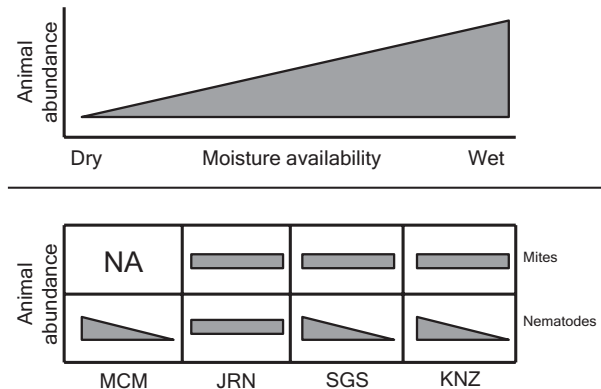


Fig. 3 Schematic diagram showing response of mite and nematode populations to changes in soil moisture availability and moisture-related environmental variables for data from both experimental manipulations and natural ecosystem gradients. Multiple regressions containing soil moisture and environmental variable data can be found in Tables S1–S4.

groups decreased within ecosystems as moisture availability increased, as did Shannon diversity and species evenness (Fig. 3, Tables S1–S3), except at JRN where no response to soil moisture or moisture-related environmental variables was observed. No response of mites to moisture availability or moisture-related environmental variables was observed within any of the ecosystems in this study. In contrast, nearly all groups of soil animals (except for bacterial-feeding nematodes) increased across the CEMG as available soil moisture (Fig. 4) and other moisture-related environmental variables increased (Shannon diversity and taxon evenness decreased, Table S4), although all groups varied in the strength of their responses relative to the moisture and environmental variables used (Table S4).

Trophic groups

All nematode trophic groups decreased with increases in soil moisture or moisture-related environmental variables within the individual ecosystems

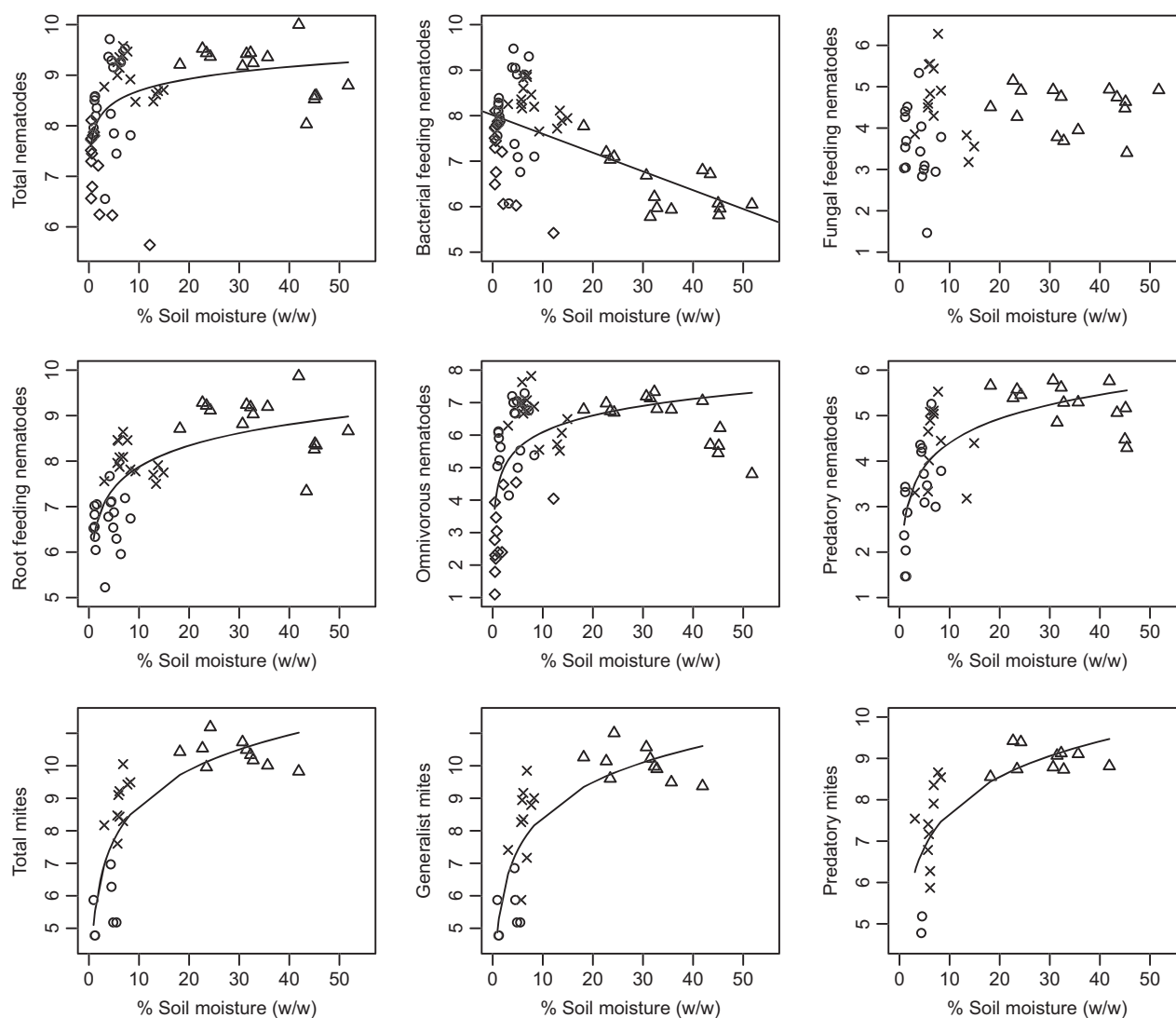


Fig. 4 Changes in total abundances of mite and nematode groups and as a response to soil moisture across the overall gradient. All abundance values are reported as $\ln(x + 1)$, with numbers of nematodes given as individuals kg^{-1} dry soil and numbers of mites given as individuals m^{-2} to a depth 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 $R^2 = 0.57^{***}$, $n = 22$. $^{***}P < 0.0001$.

used in this study (except at JRN as previously noted), and changes in the proportional abundances of nematode trophic groups led to shifts in community composition. At KNZ, increases to ANPP from 2 years prior to sampling resulted in large decreases in the proportion of bacterial-feeding nematodes and a sharp increase in root-feeding nematodes (Fig. 5a). At MCM, changes to populations of bacterial-feeding nematodes were inversely proportional to available moisture and were paired with a sharp increase in the proportion of omnivorous nematodes (Fig. 5b).

Across the CEMG, the proportion of fungal-feeding, root-feeding and predatory nematodes increased with available moisture or moisture-related variables, bacterial-feeding nematodes decreased and no response of omnivorous nematodes was observed relative to these variables (Fig. 6).

Both generalist and predatory mite abundances increased with changes to available soil moisture across the CEMG (Fig. 4), however changes in moisture availability had no effect on either group within any individual ecosystem. The proportion of

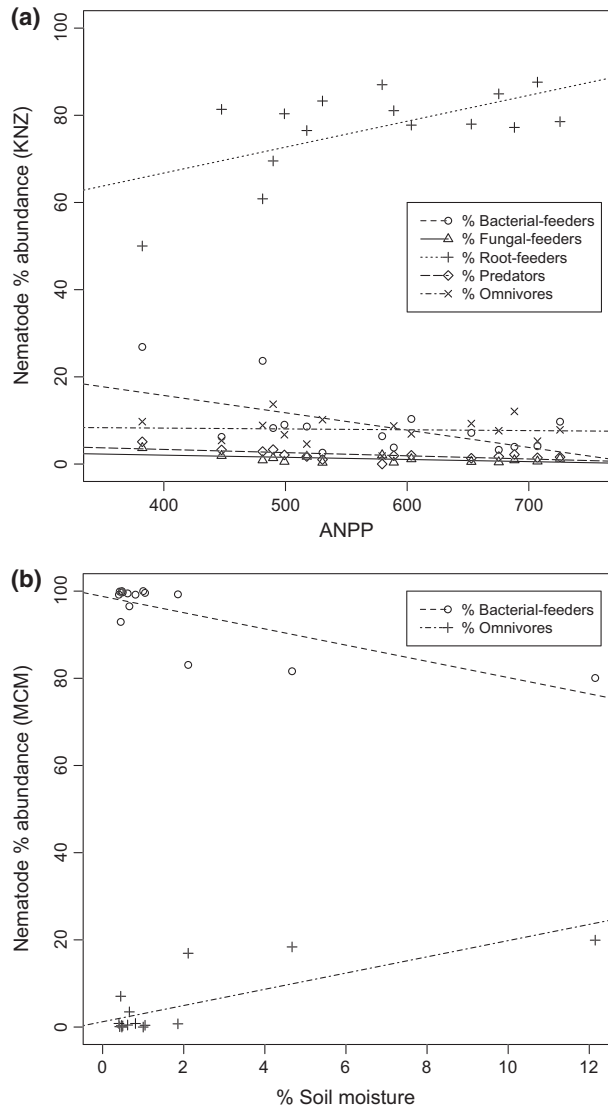


Fig. 5 Changes in proportional distribution of nematode trophic groups as a response to environmental factors with the strongest effect on all trophic groups at (a) KNZ and (b) MCM. Note that for SGS no single factor was significant for all trophic group responses and at JRN only soil physical properties 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. $^*P < 0.05$, $^{**}P < 0.001$ and $^{***}P < 0.0001$.

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 ($R^2 = 0.98$, $P = 0.0003$). In addition, the overall proportion of

mites increased relative to total nematode numbers ($R^2 = 0.45$, $P < 0.0001$).

Discussion

This study provides one of the first multi-ecosystem, cross-scale standardized investigations of how soil moisture availability can control populations of soil animals within several ecosystem types and at a larger regional/global scale (but see Petersen & Luxton, 1982; Wall *et al.*, 2008; Powers *et al.*, 2009). We show that soil animals respond to changes in moisture availability and related factors in a similar manner at local (within-ecosystem) scales and regardless of ecosystem type, but responses of these organisms differ when examined at regional/global (cross-ecosystem) 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 within individual ecosystems this effect is more gradual, linear, and generally negative in its relationship.

Within-ecosystem and cross-ecosystem (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 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. In addition, responses 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 nonlinear increases in abundance in response to 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 for soil animal activity 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 & Moorhead, 2004) further support the importance of moisture availability for these organisms. Together, these effects control soil moisture availability and therefore habitat suitability, critical for the long-term

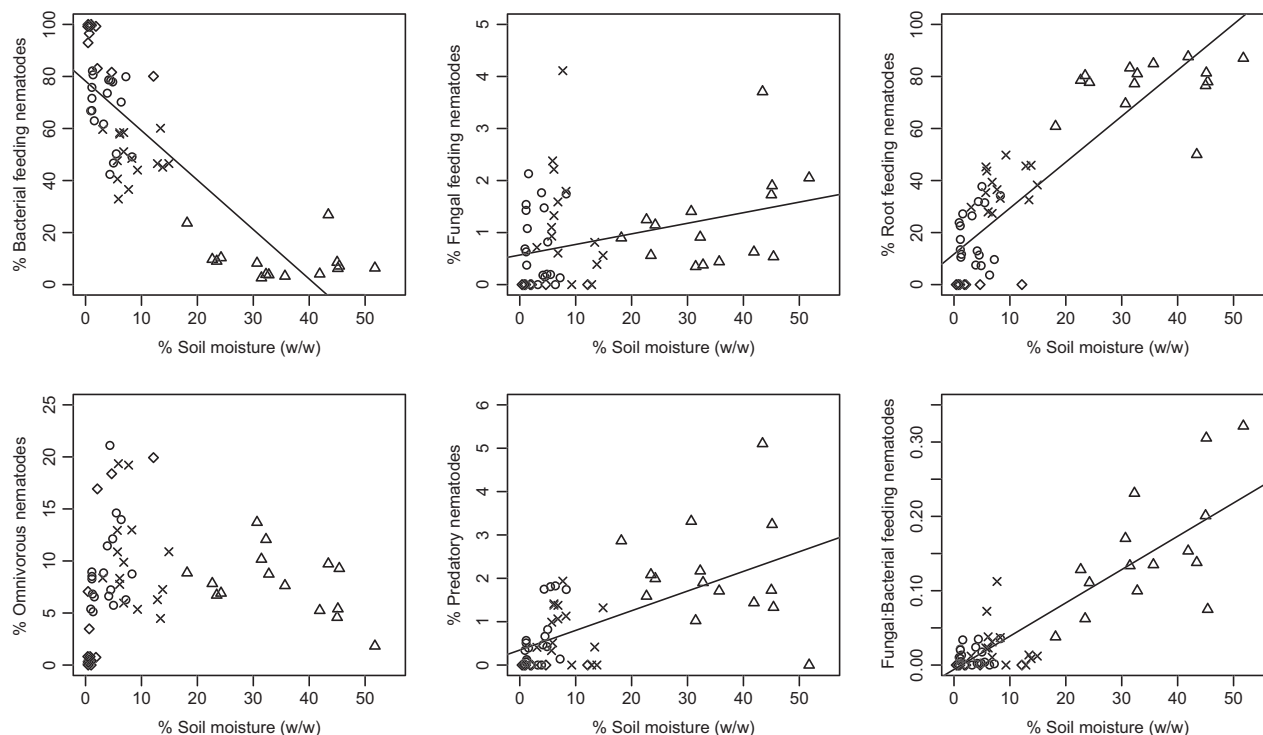


Fig. 6 Changes in proportional composition of nematode trophic groups and fungal : bacterial-feeding nematodes as a response to soil moisture across the overall gradient. Symbols for each site are open circles for JRN, open triangles for KNZ, open diamonds for MCM and crosses for SGS. % Bacterial-feeders $R^2 = 0.70^{***}$; % 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 *** $P < 0.0001$.

persistence of nematode populations in both ecosystems. Extreme climatic events or longer-term climatic presses 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). These changes to ecosystems are predicted to be more common, especially if events such as the drought affecting the midwestern United States in 2012 occur with increasing frequency in the future (Easterling *et al.*, 2000; Strzpek *et al.*, 2010). Given patterns observed in this study across the CEMG, it may be that as drought frequency increases the contributions of fungal- and root-mediated energy pathways in these ecosystems will be less important to carbon and nutrient cycling and flows through bacterial-mediated channels will increase. This can have important implications for how tightly nutrients such as nitrogen are cycled, as bacterial-mediated decomposition pathways are 'leakier' than fungal-mediated pathways (de Vries *et al.*, 2006, 2011). Decreases to the role of fungal pathways in decomposition and nutrient cycling dynamics may also influence soil structure and

storage of organic C and N within soils (Wilson *et al.*, 2009).

While environmental factors are fairly consistent within the individual ecosystem types, several factors known to influence soil animal communities such as aboveground plant species identity, quality, and cover (Porazinska *et al.*, 2003; Sylvain & Buddle, 2010; Eisenhauer *et al.*, 2012; Klass *et al.*, 2012) vary across the CEMG and may explain the different patterns in soil animal abundances and community composition observed between the CEMG and the individual ecosystems within this study. Eisenhauer *et al.* (2012) suggest root production and carbon allocation may drive changes in soil animal communities; they observed that increases in N limited carbon inputs to the soil through roots with 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 & Jackson, 2002a,b). Aboveground diversity and species identity may also potentially explain observed differences, as litter diversity (Hansen & 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. At the global scale, Wu *et al.* (2011) note that belowground diversity (eukaryotic OTUs) does not overlap well with traditionally considered aboveground diversity hotspots. This suggests that aboveground diversity plays a role in structuring soil animal communities at scales intermediate to global or local scales, with climate change resulting in shifts to species ranges and biome distributions at larger scales, potentially with large effects on environments at the local scale (Walther *et al.*, 2002; Van Der Putten *et al.*, 2010). In addition, while temperature strongly varies across the CEMG (mean annual temperature ranges from -19°C at MCM to 14.7°C at JRN), we feel that this effect is most strongly manifested through its control of soil moisture or aboveground community structuring. Other authors have investigated the effects of multiple climate drivers on soil communities and found moisture to be the strongest controlling variable on soil organisms, with temperature having either no or very weak effects (Kardol *et al.*, 2010, 2011; Darby *et al.*, 2011).

Taxa and trophic groups

Across the CEMG, mite and nematode trophic groups (excepting bacterial-feeding nematodes) responded similarly and increased in number with increased soil moisture availability. Only nematodes responded to changes in soil moisture within individual ecosystems, generally decreasing as moisture availability increased; neither group responded to moisture changes in JRN. These results partially matched our second 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 as we had predicted. Decreasing moisture can positively influence abundances of bacterial- and fungal-feeding nematodes (Wasilewska, 1991; Yeates & Bongers, 1999; Ruan *et al.*, 2012) and increases in root-feeders and omnivores have been observed with increasing precipitation (Yeates & Bongers, 1999). Decreases of all trophic group abundances with soil moisture increases within the two grassland ecosystems (KNZ and SGS) represent patterns not previously reported; other studies have demonstrated general increases in nematode numbers with increasing moisture availability, although these studies found significant effects only between complete water removal and additional irrigation (Landesman *et al.*, 2011) or over a soil moisture range more reflective of two sites (SGS to KNZ) used in our study (Kardol *et al.*, 2010) and over which range our results are comparable.

In contrast to our third hypothesis, the observed strength of responses of individual trophic groups to

changes in moisture availability did not match expected patterns. Along the CEMG, animals from higher trophic levels (predators and omnivorous nematodes) responded strongly and increased with available soil moisture while animals from lower trophic levels had variable responses; root-feeding nematodes showed strong positive responses to soil moisture availability, however bacterial-feeding nematodes demonstrated a weak decrease to available soil moisture and fungal-feeding nematodes showed no response. No clear patterns in how trophic groups responded to changing moisture emerged within the individual ecosystems: trophic groups responded idiosyncratically within each ecosystem, with animals from higher and lower trophic levels showing variable response strengths to moisture changes depending on the ecosystem studied (KNZ, MCM or SGS), while at JRN, no response of any animal group was observed with changing moisture availability. Within the wettest biome (KNZ), decreasing nematode abundances with increasing moisture may be due to prolonged habitat unsuitability from oversaturation (responses of some groups appear to decrease beyond a threshold of approximately 40% soil moisture, possibly moving conditions beyond niche suitability for organisms found at the site such as occurs for *Scottinema lindsayae* at MCM, although this was not measured for this study; Treonis *et al.*, 1999) or by altering biotic controls on nematode communities, which may be mediated through interactions with vegetation or predatory organisms not incorporated in this study, while the xeric grassland (SGS) may feature nematode communities selected via environmental filters and adapted through time to more arid conditions. Treonis *et al.* (1999) and Courtright *et al.* (2001) reported changes in community composition (but not decreases in abundance as observed in this study) in response to changing soil moisture availability at MCM. The lack of nematode responses within JRN to changes in moisture reflects earlier findings from the same site (Whitford *et al.*, 1981; Steinberger *et al.*, 1984; Freckman *et al.*, 1987), and it may be that nematode communities at JRN are highly resilient to changes in available soil moisture and comprise species that have been selected over time for tolerance to prolonged periods of drought interspersed with brief periods of wetter conditions, as observed by Demeure *et al.* (1979) when experimentally drying soils containing individuals of *Acrobeloides* sp. collected from desert soils.

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 their findings, 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 changing moisture within the individual ecosystems of this study conflict with studies finding positive responses to increased soil moisture availability (Lindberg *et al.*, 2002; Tsiafouli *et al.*, 2005; Badejo & Akinwale, 2006; Chikoski *et al.*, 2006), however these studies were all conducted in forests; an irrigation study by Kardol *et al.* (2011) in an old-field ecosystem found no effects of moisture on mites. Mite assemblages within grassland and desert systems may be more resistant to drought stress than those within forested systems: grassland and desert systems tend to have little cover provided from the litter layer to fluctuations in ambient climatic conditions, possibly favoring assemblages 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 and may account for the stronger response of these communities to drought when the system is subjected to extreme events.

Our findings suggest that changing 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 altered precipitation regimes caused by climate change, soil moisture in xeric ecosystems is projected to increase while decreasing in mesic ecosystems (Knapp *et al.*, 2008). Under these projections, our data suggest that trophic group abundances of nematode communities within xeric ecosystems may decrease, except for an increase in root-feeding nematodes (where present), increasing the amount of belowground herbivory within these systems. In contrast, in mesic ecosystems all groups except for root-feeding nematodes may increase, 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, 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 below-ground 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-ecosystem studies. Experiments at multiple ecosystems that include responses of both above- and below-ground components of terrestrial ecosystems may therefore increase the ability to predict future ecosystem dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Soil animal groups, diversity indices and best-fit model explaining changes in total abundances within KNZ.

Table S2. Soil animal groups, diversity indices and best-fit model explaining changes in total abundances within SGS.

Table S3. Soil animal groups and best-fit model explaining changes in total abundances within MCM.

Table S4. Soil animal groups, diversity indices and best-fit model explaining changes in total abundances across the CEMG.