CONCEPTS, REVIEWS AND SYNTHESES

A meta-analysis of responses of soil biota to global change

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Abstract Global environmental changes are expected to impact the abundance of plants and animals aboveground, but comparably little is known about the responses of belowground organisms. Using meta-analysis, we synthesized results from over 75 manipulative experiments in order to test for patterns in the effects of elevated CO_2, warming, and altered precipitation on the abundance of soil biota related to taxonomy, body size, feeding habits, ecosystem type, local climate, treatment magnitude and duration, and greenhouse CO_2 enrichment. We found that the positive effect size of elevated CO_2 on the abundance of soil biota diminished with time, whereas the negative effect size of warming and positive effect size of precipitation intensified with time. Trophic group, body size, and experimental approaches best explained the responses of soil biota to elevated CO_2, whereas local climate and ecosystem type best explained responses to warming and altered precipitation. The abundance of microflora and microfauna, and particularly detritivores, increased with elevated CO_2, indicative of microbial C limitation under ambient CO_2. However, the effects of CO_2 were smaller in field studies than in greenhouse studies and were not significant for higher trophic levels. Effects of warming did not depend on taxon or body size, but reduced abundances were more likely to occur at the colder and drier sites. Precipitation limited all taxa and trophic groups, particularly in forest ecosystems. Our meta-analysis suggests that the responses of soil biota to global change are predictable and unique for each global change factor.

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Introduction

Rising atmospheric CO_2 and climatic change are anticipated to alter the functioning and structure of terrestrial ecosystems (Chapin et al. 1997), and this has triggered extensive research into the consequences of these environmental changes. The majority of experiments have focused on plants and animals living aboveground (Harrington et al. 1999; Hughes 2000; Walther et al. 2002; Badeck et al. 2004; Ainsworth and Long 2005; Parmesan 2006, 2007; Stiling and Cornelissen 2007; Lenoir et al. 2008; Wu et al. 2010). Comparably less is known on responses of soil biota (Fierer et al. 2009). Soil biota influence biogeochemical cycling and physical conditions,

and their responses to global change are likely important at the ecosystem scale (Brussaard et al. 1997; Lavelle et al. 1997; Bradford et al. 2002a).

Interactions between soil organisms are inherently complex; both bottom–up and top–down forces are at play (i.e., resource supply and predation, respectively; Scheu 2002), and these interact with climate and physical factors such as available mineral surfaces (Wall et al. 2008). The ultimate controls of belowground trophic structure are still heavily debated (Scheu 2002; Wardle 2002). Most research into soil biotic responses to global change has focused on the microflora: bacteria and fungi (Zak et al. 2000; Treseder 2004; de Graaff et al. 2006). Bacteria and fungi make up most of the soil microbial biomass (Fierer et al. 2009), the turnover of which impacts nutrient cycling, distribution, and availability to plants (Ingham et al. 1985; Hunt et al. 1987; Verhoef and Brussaard 1990; Bardgett and Chan 1999), and soil aggregate stability (Wright and Upadhyaya 1998). Soil fauna at higher trophic levels, such as protozoans, nematodes, mites, and springtails, influence the activity and turnover of the microflora through grazing (Clarholm 1989; Kuikman and Van Veen 1989; Rutherford and Juma 1992; Hedlund and Öhrn 2000). Effects of global change on these higher trophic levels of the soil food web could have important consequences for C and nutrient cycling in terrestrial ecosystems, both directly through effects on population size and turnover of the microflora (Woods et al. 1982; Griffiths 1986; Kuikman et al. 1989; Wright et al. 1995) and indirectly through effects of fauna on litter comminution, soil bioturbation, and soil structure (van Vliet et al. 1995; Lavelle et al. 1997; Laakso et al. 2000; Bradford et al. 2002b; Meyer et al. 2010).

Given the complexity of the soil food web, are there any general patterns of response to environmental change? Some taxa may be more sensitive than others to particular components of global change. Bacteria, enchytraeids, nematodes, and protozoans dwell largely in water films (Jones et al. 1969; Elliott et al. 1980; Vargas and Hattori 1986; Didden 1993; Hassink et al. 1993; Bouwman and Zwart 1994; Savin et al. 2001), whereas fungi, mites, and springtails dwell in inter-aggregate voids (Petersen and Luxton 1982; Denef et al. 2001; Six et al. 2006) and tend to prefer drier conditions (Hendrix et al. 1986; Cornejo et al. 1994). Bacteria and organisms that feed on them may be less sensitive to climatic change than fungi because bacteria inside soil aggregates and other small pores (e.g., associated with clay particles) experience less extreme fluctuations in microclimate (Bushby and Marshall 1977; Hattori 1988; Denef et al. 2001). Other studies found that habitable pore space was not important in explaining the responses of bacteria and fungi to desiccation, because predators can feed in the remaining water pockets (Savin et al. 2001), bacteria and fungi have similar survival

strategies (West et al. 1992; Shi et al. 2002; Strickland and Rousk 2010), and water eventually evaporates from both small pores and large pores during drought events (Van Gestel et al. 1996). Mites may be generally less sensitive than springtails to high temperature and desiccation (Hodkinson et al. 1994; Coulson et al. 1996). It is unknown whether the varying ecological niches of taxa elicit different responses to global change. The importance of body size in explaining the responses of soil biota to elevated CO_2 and warming is also unknown. Smaller organisms can live in smaller pores that contain resources inaccessible to larger organisms (Strong et al. 2004) and that are perhaps more buffered from extreme temperatures. Body size correlates strongly with metabolic rate, generation time, population density, and food size (Peters 1983) and may provide a useful functional classification of soil biota (Verhoef and Brussaard 1990; Beare et al. 1995; Bradford et al. 2002a).

A recent meta-analysis concluded that spatial variation in soil microbial and faunal biomass is predictable across biomes, with soil biota increasing with more NPP and soil C, suggesting universal C limitation (Fierer et al. 2009). CO_2 enrichment, warming, and increased precipitation often increase plant photosynthesis and NPP (Nijs and Impens 1996; Rustad et al. 2001; Ainsworth and Long 2005; Barker et al. 2006; Del Grosso et al. 2008; Niu et al. 2008; Prieto et al. 2009; Gunderson et al. 2010; Wu et al. 2010) and are therefore likely to alleviate potential resource limitations of soil microbial groups. Warming and increased water availability can also directly stimulate soil microbial activity (West et al. 1988, 1992; Zogg et al. 1997; Gulledge and Schimel 1998; Arnold et al. 1999; Fierer and Schimel 2002). Warming can reduce soil moisture by increasing evapotranspiration (Norby and Luo 2004; Dermody et al. 2007), and CO_2 enrichment often increases soil moisture due to decreased plant stomatal conductance (Field et al. 1995; Drake et al. 1997; Morgan et al. 2004; Ainsworth and Long 2005). Experimental manipulations of CO_2 concentration, warming, and precipitation therefore provide a means to test the effects of multiple environmental constraints on belowground communities.

Experimental evidence for responses of multiple trophic levels of the soil food web to elevated CO_2 is equivocal. Elevated CO_2 generally increases the total microbial biomass (Zak et al. 2000; Allen and Schlesinger 2004; de Graaff et al. 2006) and the abundance of mycorrhizal fungi due to enhanced plant mutualism (Klironomos et al. 1996; Staddon and Fitter 1998; Treseder 2004). For higher trophic levels, responses to elevated CO_2 vary. In a greenhouse CO_2 study of a grassland soil, CO_2 effects were larger for higher trophic levels (approximately +30% for herbivores and bacterivores, and +110% for predators),

possibly because higher trophic levels were regulated by resource limitation, while lower levels remained limited by predation (Yeates et al. 1997). In a field CO_2 study of a different grassland soil, elevated CO_2 had no effect on the abundance of herbivorous nematodes, the abundance of grazers (i.e., protozoans, bacterivorous and fungivorous nematodes, mites, and springtails), or total microbial biomass, and there were fewer large predacious nematodes possibly due to smaller soil aggregate size (Niklaus et al. 2003). Therefore, the effects of elevated CO_2 on soil biota may depend on trophic group and body size.

Effects of experimental warming and altered precipitation on soil biota are also equivocal. In four heathland ecosystems along a climatic gradient in Europe, experimental warming tended to increase soil microbial biomass at the coldest and wettest site (i.e., cold limitation), and decrease soil microbial biomass at the warmest and driest site (i.e., heat and water stress; Sowerby et al. 2005). In some ecosystems, mites respond more strongly to warming than springtails (Sjursen et al. 2005; Bokhorst et al. 2008); in other ecosystems, springtails respond more strongly to warming than mites (Convey et al. 2002; Sinclair 2002; Haimi et al. 2005; Bokhorst et al. 2008), perhaps due to dissimilar ecological requirements in different ecosystems. Increasing precipitation resulted in fewer mites and more springtails in a high arctic tundra (Coulson et al. 2000), and the responses of soil fauna to increased and reduced precipitation are not necessarily symmetrical (Lindberg et al. 2002; Tsiafouli et al. 2005). Thus, there is evidence that the effects of climatic change on soil biota depend on taxonomy, ecosystem type, local climate, and the direction of precipitation change.

Here, we used meta-analysis to test whether there are general patterns of response of soil biota to global environmental change. The present analysis is based on a classification of soil biota into broad taxonomic and functional groups. This classification was chosen for two reasons. First, as discussed above, taxonomic groups differ in ecological requirements and soil physical niches, and may therefore differ in their response to global change. Second, trophic dynamic theory (e.g., Hairston et al. 1960; Scheu 2002) suggests that trophic levels differ in limitations, and may therefore exhibit specific responses to global change that may propagate up or down the food web.

Our first objective was to quantify the effects of CO_2 enrichment, experimental warming, and altered precipitation on the abundance of soil biota to determine whether any global change factor was particularly influential. Our second objective was to determine whether the responses of soil biota to global change were correlative with taxonomy, body size, or trophic level. Our third objective was to assess the importance of ecosystem type, local climate,

and experimental approach in explaining the responses of soil biota to global change.

Materials and methods

Data collection

Inference from meta-analysis depends on selection criteria (Hungate et al. 2009). Our meta-analysis includes over 150 measurements of the abundance or biomass of soil organisms in longer-term experiments (i.e., >50 days) that simulated an increase in atmospheric CO_2 concentration in the field or greenhouse (Online resource 1), an increase in temperature in the field (i.e., 'warming'; Online resource 2), and an increase or reduction in precipitation quantity in the field (Online resource 3). To investigate more realistic global changes, our data collection of warming and precipitation studies excluded laboratory experiments, which tend to reflect responses to short-term changes in temperature and moisture rather than a shift in climate, and because laboratory studies use disturbed soil rather than intact profiles. Greenhouse CO_2 studies were included in this analysis because simulating a realistic increase in atmospheric CO_2 concentration in plant–soil mesocosms is achievable, more so than simulating diurnal and seasonal variation in temperature and the quantity and frequency of precipitation events. In addition, there are a large number of greenhouse CO_2 studies, and much time has been invested in setting up these manipulations, and it is unknown whether responses of soil biota in the greenhouse approximately match field responses.

Abundance measurements (i.e., density) were used in this meta-analysis whenever possible, but biomass measurements were included as a surrogate for abundances (Petersen and Luxton 1982), and henceforth 'abundance' refers to both abundance and biomass measurements. Bacteria, protozoans, springtails, mites, enchytraeids, nematodes, and macroarthropods were typically measured as the number of individuals per unit area or per gram of soil. Total microbial biomass was measured as $\mu g\ C\ g^{-1}$ soil while measurements of fungi varied (e.g., hyphal length, % colonization, spore count, PLFA biomass, and relative gene abundance).

Treatment and control means, errors, and sample sizes (n) were recorded for each measurement. Search engines (Google Scholar and ISI Web of Knowledge) and cross-referencing were used to find studies in the literature that met these criteria. Search terms included global change, climate change, elevated CO_2, temperature, warming, or precipitation and soil biota, belowground organisms, microbial biomass, or taxon names. Taxa represented in the literature with multiple replicates included bacteria

(domain Bacteria), fungi (kingdom Fungi), protozoans (kingdom Protista), springtails (subclass Collembola), mites (subclass Acari), enchytraeids (family Enchytraeidae), nematodes (phylum Nematoda), and macroarthropods (phylum Arthropoda). Microbial biomass is commonly assessed in global change experiments, and measurements were included to primarily reflect abundances of bacteria and fungi, because they account for up to 96% of belowground heterotrophic biomass (Anderson and Domsch 1978; Van Veen and Paul 1979; Fierer et al. 2009). Taxa were assigned to body width classes according to the literature (Verhoef and Brussaard 1990; Beare et al. 1995): microflora and microfauna (1–100 μm wide: Bacteria, Fungi, Protozoa, Nematoda, and total microbial biomass); mesofauna (100 μm–2 mm wide: Acari, Collembola, and Enchytraeidae), and macrofauna (2–20 mm wide: macroarthropods).

To ensure some degree of independence between measurements, if multiple species or trophic groups were measured from a single taxon within a given study, then an overall mean for the three most abundant species in the taxon was calculated (if authors did not do so already). If a taxon was measured more than once in the same experiment (i.e., multiple sampling dates), then the measurement with the longest treatment duration was included. If a taxon was measured in multiple soil horizons, then the measurement from the soil horizon with the highest population density in the control treatment was included (e.g., organic horizon microbial biomass in Bradford et al. 2008).

In order to minimize bias associated with land management (e.g., fertilization, tillage, and livestock grazing), only manipulative experiments performed in natural or relatively unmanaged soils were included in this meta-analysis. Ecosystems were classified according to vegetation type and climate as boreal forest, coniferous forest (temperate), deciduous forest (temperate), desert (hot), grassland, heathland, shrubland, tropical forest, or tundra. We included measurements from multiple sites in the same study as long as treatments were replicated and that the author(s) defined a distinct difference in geography (e.g., 'Anchorage Island' and 'Signy Island'), parent material (e.g., 'serpentine' and 'sandstone'), microclimate (e.g., 'wet' and 'dry'), or vegetation (e.g., 'heathland' and 'tundra').

Commonly reported categorical variables chosen to possibly explain variation in global change effects included the taxon and body width class of soil biota, and the type of ecosystem sampled. Four continuous variables from each study were also recorded: the mean annual temperature (MAT) and mean annual precipitation (MAP) of study sites where soils were collected, and the magnitude (CO_2: +ppmv above standardized ambient concentration of 370 ppmv; warming: temperature in °C; precipitation: increase or reduction) and duration of treatments (in years).

Trophic level as a grouping variable

Because of the substantial number of CO_2 and precipitation studies that have measured multiple soil trophic groups within a taxon (e.g., different nematode species that primarily eat bacteria or fungi), the body of knowledge on common feeding habits of different taxa of soil biota (e.g., Petersen and Luxton 1982; Yeates et al. 1993), and the hypothesized influence of precipitation (Lensing and Wise 2006) and CO_2 enrichment on soil food webs (Klironomos et al. 1997; Yeates et al. 1997, 2003; Hoeksema et al. 2000; Hungate et al. 2000; Neher et al. 2004; Sonnemann and Wolters 2005; Drigo et al. 2008), we modified the dataset to a form suited to test for common changes in trophic structure among different taxa. A trophic group, or feeding group, consists of biological species or taxa that depend on similar prey or substrates, and that are assumed to be functionally equivalent in the food web (Scheu 2002). Species that consume detritus (detritivores), live plant roots (herbivores), bacteria (bacterivores), fungi (fungivores), and soil fauna (predators) were assigned to separate trophic groups.

There were no warming studies in our dataset in which authors defined the feeding preferences of measured organisms, but there were nine measurements of mites and nematodes in CO_2 enrichment studies with defined trophic groups for different species (Klironomos et al. 1997; Yeates et al. 1997; Hoeksema et al. 2000; Hungate et al. 2000; Niklaus et al. 2003; Neher et al. 2004; Sonnemann and Wolters 2005) and six measurements of nematodes and macroarthropods in precipitation studies (Freckman et al. 1987; Todd et al. 1999; Bakonyi and Nagy 2000; Lindberg et al. 2002; Lindberg and Persson 2004). The dataset was expanded to incorporate these means and errors for different trophic groups (Online resource 4; Online resource 5). When the feeding preference of a taxon was not defined by the author(s), the measurement was either removed or defined for the purpose of this meta-analysis based on general patterns found in the literature. Bacteria, Fungi, and microbial biomass were defined as detritivores, Collembola were defined as primarily fungivores (Hunt et al. 1987; Bardgett et al. 1993; Chen et al. 1996; Briones et al. 1999), and Protozoa were defined as bacterivores (Ingham et al. 1986; Hunt et al. 1987; Brussaard 1998). Because of the more omnivorous feeding habits of Acari, Enchytraeidae, Nematoda, and macroarthropods (Hunt et al. 1987; Didden 1993; Yeates et al. 1993; Ponsard and Arditi 2000), the authors must have defined a feeding group for measurements of these taxa to be included in this separate trophic meta-analysis. As a result, seven measurements of Acari, Enchytraeidae, and Nematoda were removed from the CO_2 dataset, and 16 measurements of Acari, Enchytraeidae, and Nematoda were removed from the precipitation dataset.

Effect size metric

We used the natural log of the response ratio (lnR) as a metric of effect size (Treseder 2004; Jastrow et al. 2005; de Graaff et al. 2006; Stiling and Cornelissen 2007; Wu et al. 2010), a metric that reflects a relative change in the abundance of soil biota due to global change treatments:

$$\ln R = \ln(T/C) \tag{1}$$

where T is the treatment mean and C the control mean. If a treatment increased the abundance of an organism (significantly or not) then the effect size lnR was greater than zero. If a treatment decreased the abundance of an organism, then lnR was less than zero. A reversal marker ($-$) was used in the precipitation dataset to standardize for effects of treatments that simulated a reduction in precipitation (i.e., control treatment became increased precipitation treatment and reduced precipitation treatment became control treatment). This effect size metric is not influenced by differences in variance between studies (e.g., Hedges' d) and focuses on equilibrial responses based on state variables, rather than rate responses based on time (Osenberg et al. 1997). However, Hedges' d provided qualitatively similar results (data not shown). The mean and variance of lnR were calculated using MetaWin 2.1 software (Rosenberg et al. 2000) with sample size as the weighting function.

Data analysis

Random-effect models were fitted for each treatment (CO_2, warming, and precipitation) by grouping variable combinations. We tested a total of five categorical variables (taxon, body size, trophic group, ecosystem type, and the direction of precipitation change) and four continuous variables (MAT, MAP, duration of treatment, and the magnitude of CO_2 and warming increase) using MetaWin 2.1 software. Because of the wide variation in manipulations employed in precipitation treatments and their efficacy (Weltzin et al. 2003), and thus the difficulty in standardizing the magnitudes of different treatments, precipitation was tested as a categorical variable (i.e., increase or decrease).

A random-effect model was chosen under the assumption that there was no single true effect size for each treatment and that there was random variation among studies in a class, in addition to sampling variation (Rosenberg et al. 2000). $P(\chi^2)$ was the probability value from a Chi-square test and the reported P value was from randomization tests with 999 iterations. The mean effect sizes ($\pm$bootstrapped 95% confidence interval) of significant grouping variables were compared to identify the particular responses driving the overall treatment effects.

Results

Differences between global change factors

When averaged across all taxa and ecosystem types, soil biota responded more strongly to altered precipitation (lnR = 0.24 $\pm$ 0.17; 11–51% increase in abundances) than to CO_2 enrichment or warming (Fig. 1). Overall responses to CO_2 enrichment (lnR = 0.02 $\pm$ 0.07; 5% decrease to 9% increase in abundances) and warming (lnR = $-$0.02 $\pm$ 0.12; 13% decrease to 11% increase in abundances) were not significantly different from zero. There was no correlation between sample size and effect size for any of the global change factors, and the effect sizes for all treatments followed a near-normal distribution (data not shown).

Responses to elevated CO_2

Responses of soil biota to elevated CO_2 did not depend on taxon or ecosystem type (Tables 1 and 2), and were not significantly correlated with MAT, MAP, or the magnitude of CO_2 enrichment (Table 3). The effects of CO_2 did depend on body width size: microflora and microfauna responded positively to elevated CO_2 and the mesofauna tended to respond negatively. The duration of CO_2 enrichment was also a significant predictor of effect sizes. The effects of elevated CO_2 on soil biota were larger in short-term experiments, with the switch from higher
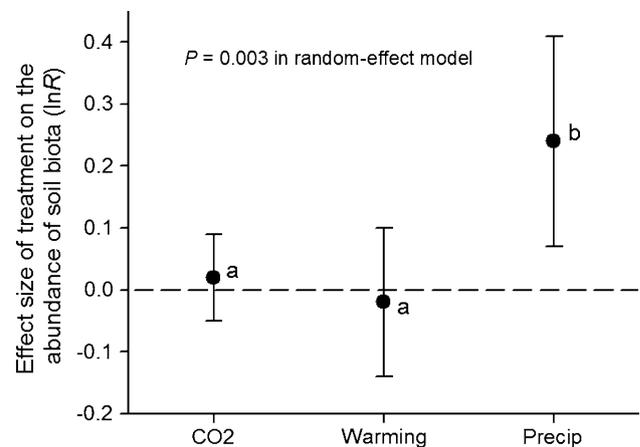
Fig. 1 The mean effect size ($\pm$bootstrapped 95% CI) of CO_2 enrichment ($n = 68$), warming ($n = 54$), and increasing precipitation ($n = 47$) on the abundance of soil biota. Means and confidence intervals include all taxa and ecosystem types; lnR = log of the response ratio = ln (treatment mean/control mean); *dotted line* indicates no response, lnR > 0 indicates increased abundances, and lnR < 0 indicates decreased abundances; *letters* indicate significant differences in Tukey's HSD test; a reversal marker was used in MetaWin 2.1 for precipitation studies (see explanation in "Materials and methods")

Table 1 Results from random-effect models of the abundance of soil biota in elevated CO_2, warming, and altered precipitation studies with the log of the response ratio ($\ln R$) as the effect size and four categorical grouping variables: the taxon of soil biota, the body width class of soil biota, the trophic group of soil biota, and the ecosystem type

Model	df	Q	Q_B/Q_T	P (χ^2)	P value
Elevated CO_2					
Taxon	7	16.05	0.08	0.021	0.49
Residual	60	195.65			
Total	67	211.70			
Body width class	1	15.14	0.05	0.0001	0.028*
Residual	66	263.62			
Total	67	278.76			
Trophic group	4	24.29	0.09	0.0004	0.041*
Residual	78	256.89			
Total	82	281.18			
Ecosystem type	4	1.03	0.004	0.90	0.98
Residual	63	235.02			
Total	67	236.05			
Warming					
Taxon	6	7.36	0.06	0.29	0.71
Residual	47	107.68			
Total	53	115.05			
Body width class	1	0.0001	<0.01	0.99	0.99
Residual	52	137.78			
Total	53	137.78			
Ecosystem type	5	19.31	0.15	0.002	0.11
Residual	48	109.55			
Total	53	128.86			
Altered precipitation					
Taxon	7	12.51	0.16	0.12	0.70
Residual	39	65.97			
Total	46	78.48			
Body width class	2	5.72	0.04	0.057	0.38
Residual	44	131.05			
Total	46	136.78			
Trophic group	3	8.70	0.11	0.032	0.22
Residual	31	72.86			
Total	34	81.56			
Ecosystem type	5	49.65	0.32	<0.001	0.008*
Residual	40	106.07			
Total	45	155.72			

The taxa were Acari, Arthropoda (macro), Bacteria, Collembola, Enchytraeidae, Fungi, Nematoda, and Protozoa; the body width classes were microflora/fauna (1–100 μm wide), mesofauna (100 μm–2 mm wide), and macrofauna (2–20 mm wide); the trophic groups were detritivores, (root) herbivores, bacterivores, fungivores, and predators; ecosystem types were defined according to vegetation as boreal forest, (hot) desert, heathland, grassland, shrubland, temperate coniferous forest, temperate deciduous forest, tropical forest, or tundra; $Q_{Between}/Q_{Total}$ (Q_B/Q_T) describes the proportion of total variation explained by each variable; $P(\chi^2)$ is the probability value for a χ^2 test and the P value is the probability value for randomization tests with 999 iterations using MetaWin 2.1 and sample size as the weighting function; see rationale in "Materials and methods" for not testing trophic group among warming studies

* Significant at an alpha level of 0.05

($\ln R > 0$) to lower abundances ($\ln R < 0$) occurring after 3.7 years. Increased abundances across taxa were also more likely to occur in greenhouse CO_2 experiments ($n = 32$; mean $\ln R$ and bootstrapped 95% CI = 0.11 and −0.004 to 0.21, respectively) than in field CO_2 experiments ($n = 36$; mean $\ln R$ and bootstrapped 95% CI = −0.04 and −0.11 to 0.02, respectively; $P = 0.007$ in random-effect model). There was no correlation between CO_2 effects and treatment duration when field and greenhouse studies were analyzed separately, indicating that experimental approach was partly responsible for the overall correlation between CO_2 effects and treatment duration. Taxon, ecosystem type, MAT, MAP, and treatment magnitude did not significantly explain the effects of CO_2 when field and greenhouse studies were analyzed separately (data not shown).

Responses to elevated CO_2 also depended on trophic group (Table 1). Elevated CO_2 significantly increased the abundance of detritivores but had no effect on the abundances of herbivores, bacterivores, fungivores, or predators (Table 2). When the trophic analysis of CO_2 effects included nematodes only ($n = 34$) and nematodes in field studies only ($n = 30$), trophic group had no effect ($P = 0.63$ and 0.69, respectively).

Responses to warming

Responses of soil biota to warming treatments did not depend on taxon, body width class, or ecosystem type (Table 1), and were best explained by MAT and MAP (Table 3). Warming was more likely to decrease the abundance of soil biota in soils collected from sites with a lower MAT and lower MAP. The logarithmic regression between MAP and responses to warming switched from negative ($\ln R < 0$) to positive effect sizes ($\ln R > 0$) at 626 mm of precipitation year^{-1} ($y = 0.41\text{Ln}(x) - 2.64$; $r^2 = 0.13$; $P = 0.002$). There was a positive correlation between MAT and MAP for the sites included in this analysis ($P = 0.008$; $r^2 = 0.22$). Responses of soil biota to warming were not significantly explained by the magnitude of temperature increase, but were negatively correlated with treatment duration (Table 3). Negative effects of warming were more likely to occur in longer-term experiments.

Responses to altered precipitation

The positive effect of precipitation on the abundance of soil biota was similar among taxa, body width classes, and trophic groups, but differed between ecosystem types (Table 1). Precipitation increased abundances of soil biota across taxa in boreal forests, coniferous forests, and deciduous forests, but had no effect in grassland, heathland,

Table 2 Mean responses (lnR) and bootstrapped 95% confidence intervals for the effects of elevated CO₂, warming, and increasing precipitation on the abundance of soil biota in different taxa, body width classes, trophic groups, and ecosystem types

Variables	Elevated CO_2			Warming			Altered precipitation		
	n	Mean	Bootstrapped CI	*n*	Mean	Bootstrapped CI	*n*	Mean	Bootstrapped CI
Taxon									
Acari	5	−0.20	−0.52 to 0.03	11	0.02	−0.49 to 0.48	10	0.22	−0.14 to 0.71
Arthropoda (macro)	–	–	–	–	–	–	3	0.41	−0.24 to 1.51
Bacteria	8	0.04	−0.06 to 0.15	5	−0.16	−0.38 to −0.02[a]	2	0.17	−0.05 to 0.40
Collembola	5	−0.15	−0.66 to 0.43	12	−0.16	−0.42 to 0.04	9	0.57	0.24 to 0.93[a]
Enchytraeidae	4	−0.14	−1.30 to 0.41	4	0.36	−0.40 to 1.15	4	0.90	0.06 to 1.74[a]
Fungi	18	0.05	−0.05 to 0.14	13	0.04	−0.16 to 0.25	4	0.25	0.08 to 0.47[a]
MB	14	0.11	0.03 to 0.20[a]	7	−0.03	−0.39 to 0.28	9	0.03	−0.31 to 0.41
Nematoda	12	0.01	−0.14 to 0.15	2	0.08	0.02 to 0.26[a]	6	0.37	−0.16 to 0.91
Protozoa	2	0.10	−0.07 to 0.22	–	–	–	–	–	–
Body width class									
Microflora/fauna	54	0.05	0.0008 to 0.11[a]	27	−0.02	−0.15 to 0.12	21	0.17	−0.02 to 0.41
Mesofauna	14	−0.14	−0.46 to 0.14	27	−0.02	−0.25 to 0.25	23	0.45	0.16 to 0.78[a]
Macrofauna	–	–	–	–	–	–	3	0.38	−0.24 to 1.51
Trophic group									
Detritivore	40	0.06	0.01 to 0.11[a]	–	–	–	15	0.12	−0.12 to 0.35
Herbivore	9	0.18	−0.13 to 0.40	–	–	–	–	–	–
Bacterivore	12	0.06	−0.09 to 0.16	–	–	–	3	−0.07	−0.43 to 0.20
Fungivore	14	−0.10	−0.33 to 0.14	–	–	–	12	0.43	0.15 to 0.77[a]
Predator	8	0.27	−0.36 to 0.52	–	–	–	5	0.36	−0.09 to 0.97
Ecosystem type									
Boreal forest	–	–	–	9	−0.10	−0.40 to 0.23	11	0.48	0.13 to 0.94[a]
Coniferous forest	18	−0.01	−0.17 to 0.12	2	0.64	0.19 to 1.01[a]	9	1.04	0.60 to 1.46[a]
Deciduous forest	13	0.04	−0.16 to 0.19	4	−0.22	−0.62 to −0.03[a]	5	0.26	0.07 to 0.45[a]
Grassland	31	0.03	−0.05 to 0.12	13	0.15	−0.06 to 0.41	9	−0.01	−0.20 to 0.20
Heathland	–	–	–	11	0.07	−0.14 to 0.27	8	−0.01	−0.37 to 0.43
Shrubland	4	0.05	−0.13 to 0.28	–	–	–	–	–	–
Tropical forest	2	0.11	−0.41 to 0.47	–	–	–	–	–	–
Tundra	–	–	–	15	−0.20	−0.47 to 0.04	8	−0.01	−0.37 to 0.43

lnR = ln (treatment mean/control mean); *n* number of observations from studies; *MB* total microbial biomass; '−' variable was untested because fewer than two observations were available or there was insufficient information to assign a trophic group; a reversal marker was used in MetaWin 2.1 for precipitation studies

[a] Bootstrapped 95% CI is significantly different from zero

or tundra ecosystems (Table 2). Effects of altered precipitation were invariant with MAP, but decreased with MAT and increased with treatment duration (Table 3).

The direction of precipitation change was also an important predictor of responses of soil biota to altered precipitation. The largest effects of precipitation in forest ecosystems occurred in drought treatments. In forest ecosystems, effects of precipitation on the abundance of soil biota were larger in drought studies (lnR bootstrapped 95% CI = 0.67–1.43; mean = 1.06; n = 14) than in irrigation studies (lnR = −0.03 to 0.31; mean = 0.15; n = 11; P = 0.002 in random-effect model; Q_B/Q_T = 0.39). In non-forest ecosystems, effects of precipitation were not

significantly different from zero, and were similar among drought studies (lnR = −0.20 to 0.32; mean = 0.04; n = 11) and irrigation studies (lnR = −0.23 to 0.12; mean = −0.06; n = 11; P = 0.57 in random-effect model).

Discussion

Biological and morphological differences among taxa affect the spatial and temporal distribution of organisms in the soil profile and within soil aggregates (Petersen and Luxton 1982; Lavelle et al. 1997; Briones et al. 2007), but

Table 3 Relationships between the effects of elevated CO_2, warming, and altered precipitation on the abundance of soil biota (lnR) and four continuous experimental variables

Treatment	Variables	Range	Mean	Intercept	Slope	r^2	P value
Elevated CO_2	Mean annual temperature (°C)	1–22	10.3	0.08	−0.006	0.009	ns
	Mean annual precipitation (mm year^{-1})	325–2,132	861	−0.02	0.0001	0.001	ns
	Magnitude of treatment (ppm)	74–390	273	−0.003	0.0001	0.0007	ns
	Duration of treatment (years)	0.2–8	2.6	0.11	−0.03	0.05	0.028*
Warming	Mean annual temperature (°C)	−7 to 16	3.2	−0.11	0.02	0.08	0.019*
	Mean annual precipitation (mm year^{-1})	119–2,250	646	−0.26	0.0004	0.11	0.004*
	Magnitude of treatment (°C)	0.4–5	2.2	0.09	−0.03	0.008	ns
	Duration of treatment (years)	0.2–15	4.2	0.09	−0.02	0.04	0.007*
Altered Precip.	Mean annual temperature (°C)	−5 to 17	7.9	0.44	−0.02	0.01	0.004*
	Mean annual precipitation (mm year^{-1})	211–2,197	965	0.15	0.0002	0.01	ns
	Duration of treatment (years)	0.1–13	3.4	0.24	0.01	0.01	0.001*

Results are from 11 separate random-effect models using MetaWin 2.1 and include soil biota from all taxa, body width classes, and ecosystem types; P value is from the regression χ^2 test; see rationale in "Materials and methods" for not testing the magnitude of precipitation treatments as a continuous variable

ns Not significant

* Significant at an alpha level of 0.05

there was little evidence that these differences were related to their responses to global environmental change. Organisms of all taxa and body sizes were limited by precipitation and showed no overall response to warming. The exception, when body size did matter, was that the microflora and microfauna responded positively to elevated CO_2, whereas the mesofauna tended to respond negatively. A possible explanation for this pattern is that smaller organisms were able to access smaller soil pores that contained readily decomposable C (Strong et al. 2004) and higher water content due to elevated CO_2 (Field et al. 1995). Another explanation may be that increased soil aggregation with elevated CO_2 (Six et al. 2001) creates a more stable microhabitat for bacteria and fungi, and ultimately promotes greater spatial separation between predators and prey (Wright et al. 1995).

Effects of elevated CO_2 on the abundance of soil biota were related to trophic structure, as expected. The detritivores responded positively to elevated CO_2, whereas the higher trophic levels showed no response. Therefore, functional classification (i.e., trophic group and body size) proved more useful than taxonomic classification in explaining responses to elevated CO_2 (Scheu and Falca 2000) and there was no evidence of a bottom-up multi-trophic response that has been suggested to be important in soil food webs with rising CO_2 (Yeates et al. 2003). Instead, predation and omnivory could generally limit the abundance of soil fauna (Petersen and Luxton 1982; Vargas and Hattori 1986; Scheu 2002). It is also possible that the response of detritivores to elevated CO_2 was related to increased water availability because altered precipitation induced a similar response among detritivores in our meta-

analysis. Fungi and fungivores responded positively to precipitation, and predators tended to respond positively, demonstrating a potential bottom–up trophic response to increased water availability. Contrary to our expectations, increasing precipitation generally favored the fungal component of the soil food web, and CO_2 enrichment favored the bacterial component.

Vegetation played a role in determining the degree to which soil biota responded to altered precipitation. In non-forest ecosystems, soil biota were less limited by drought, and probably more limited by C availability. However, in forest ecosystems, abundances of soil biota were strongly limited by low precipitation, particularly in drought treatments. Thus, adding a resource elicits a qualitatively different response than reducing the resource in an already constrained ecosystem. The reason for this pattern is unknown, but may be related to a physical effect of precipitation on litter comminution (Lensing and Wise 2007), the degree of water limitation in the litter layer versus mineral horizons (Keith et al. 2010), or a competition for water between trees and soil biota under low water availability (Odhiambo et al. 2001). Another possible explanation for the difference between forest and non-forest responses to precipitation is that we included measurements of abundances from the soil horizon with the highest population density (if abundances for more than one horizon were reported), which tended to be the organic layer for forest ecosystems, and the organic layer is more susceptible than mineral soil to desiccation (Keith et al. 2010).

Climate best explained the effects of experimental warming on soil biota. According to the studies included in our meta-analysis, warming is more likely to reduce the

abundances of soil biota in colder and drier climates. Negative effects of warming may mean that the organisms are avoiding the heat and living deeper in unsampled soils (Briones et al. 2007), experiencing water stress (Hodkinson et al. 1994; Kardol et al. 2011), or dying off due to heat stress (Coulson et al. 1996; Bokhorst et al. 2008; Briones et al. 2009). It is also possible that the community composition is altered by warming, with fewer cold-adapted (Coulson et al. 1996) or wet-adapted species (Kardol et al. 2011). Negative effects of warming in drier climates suggest an important interaction between future changes in temperature and water availability, whereby warming-induced drying will exacerbate water limitation on belowground populations in arid and semiarid ecosystems. In contrast to aboveground biota (Gerten et al. 2008), positive effects of precipitation on soil biota were just as likely to occur in wetter climates as in drier climates, indicating that water availability generally limits the abundance of soil organisms across climatic zones.

The effects of all three global change factors considered in this meta-analysis varied with treatment duration. Positive effects of elevated CO_2 were more likely to occur in short-term experiments. The switch in responses after 3 years of CO_2 enrichment (i.e., from positive to no response) is similar to the temporal trend found with NPP (Oren et al. 2001) and N fixation (Hungate et al. 2004), and could reflect a recovery period after perturbation (Luo 2001) and a shift from C limitation to nutrient limitation (Luo et al. 2004). Negative effects of warming were more likely to occur in long-term experiments, which may reflect an initial relief of cold limitation on certain species (Ruess et al. 1999; Cole et al. 2002; Convey and Wynn-Williams 2002) followed by long-term water limitation associated with warming-induced drying (Harte et al. 1996; Sinclair 2002; Aerts 2006). Soil respiration also exhibits a transient response to warming (Luo et al. 2001) associated with a reduction in microbial C use efficiency (Allison et al. 2010) and a pulse of readily decomposable C that is eventually exhausted (Kirschbaum 2004). Positive effects of increasing precipitation on soil biota were larger in long-term experiments, suggesting that permanent changes in water availability cause permanent changes in population sizes. We find it particularly striking that the effects of elevated CO_2 diminished with time, whereas the effects of warming and altered precipitation intensified with time. The transient disequilibria caused by step responses of soil biota to CO_2 enrichment should be interpreted with caution in experiments shorter than 3 years. On the other hand, the long-term responses of soil biota to factors that show natural variation (i.e., temperature and precipitation) seem to be more gradual and directional.

Greenhouse CO_2 studies overestimated the responses of soil biota observed in the field. This difference may reflect an initial release of soil C by physical disturbance and seedling establishment in mesocosms, which can have ramifications up to 3 years later (Rygiewicz et al. 2010), and environmental stress is generally lower in greenhouse studies and can lead to the detection of effects not occurring in the field (Peters 1993; Goverde et al. 2002). Also, the greenhouse studies in our meta-analysis were conducted for approximately 1 year, on average, and primarily captured the short-term response to elevated CO_2, whereas field experiments (4 years, on average) captured the long-term response. Therefore, more long-term CO_2 studies are needed. We found no evidence that higher magnitudes of CO_2 enrichment or warming caused larger effects on belowground population sizes (Klironomos et al. 2005), supporting the ecological relevance of both step and gradual global change manipulations (Luo 2001).

The patterns found in our meta-analysis indicate that elevated CO_2, warming, and altered precipitation affect soil biota to different degrees. Effects of elevated CO_2 depended most on trophic structure and body size, whereas effects of warming and altered precipitation depended on local climate and ecosystem type. Two mechanistic constraints on soil biota emerged from this synthesis. First, the abundance of soil biota is generally limited by water availability; the mean effect of precipitation was positive for all taxa included in this analysis and much larger than the mean effects of elevated CO_2 and warming. Second, the abundance of biota in cold and dry soils is limited by temperature.

These general patterns serve as hypotheses for the mechanisms that drive the responses of soil biota to global environmental change, and may help us predict when particular changes in abundances of soil biota will impact ecosystem functioning. We have also identified research gaps. For example, measurements of macrofauna are needed in CO_2 and warming studies, trophic measurements are needed in warming studies, measurements of bacteria and protozoans are needed in precipitation studies, and all measurements are needed in tropical ecosystems. Measurements of the abundance of soil biota in global change experiments provide a useful context through which to study the general mechanistic constraints on belowground communities. Our meta-analysis suggests that simultaneous changes in atmospheric CO_2 concentration and climate will influence multiple environmental constraints on belowground communities. For example, detritivores are predicted to respond most strongly to a simultaneous increase in CO_2 concentration, temperature, and precipitation in relatively cold and dry forest ecosystems. Interactions between different global change factors may create responses not predicted by single-factor experiments (Shaw et al. 2002; Norby and Luo 2004); therefore, more multifactor experiments are needed.

Other remaining challenges include our ability to relate quantitative changes in abundances of soil biota to decomposition, soil C storage, nutrient mineralization, plant production and diversity, and energy transfer to aboveground food webs. These challenges exist for ecologists in relatively unmanaged ecosystems, as well as in agricultural and rangeland ecosystems where abundances of different taxa or trophic groups may be managed to maximize fertilization efficiency and minimize root herbivory and parasitism. Furthermore, our meta-analysis was focused on abundance measurements and did not consider the effects of global change on the community composition of individual taxa and trophic groups (Cragg and Bardgett 2001). Functional dissimilarity within a trophic group (e.g., a diverse set of enzymes among detritivores) can be just as important as species richness and population size for ecosystem functioning (Heemsbergen et al. 2004).

References

Aerts R (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. J Ecol 94:713–724

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol 165:351–372

Allen AS, Schlesinger WH (2004) Nutrient limitations to soil microbial biomass and activity in loblolly pine forests. Soil Biol Biochem 36:581–589

Allison SD, Wallenstein MD, Bradford MA (2010) Soil–carbon response to warming dependent on microbial physiology. Nature Geosci 3:336–340

Anderson JPE, Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol Biochem 10:215–221

Arnold SS, Fernandez IJ, Rustad LE, Zibilske LM (1999) Microbial response of an acid forest soil to experimental soil warming. Biol Fert Soils 30:239–244

Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, Schaber J, Sitch S (2004) Responses of spring phenology to climate change. New Phytol 162:295–309. doi:10.1111/j.1469-8137.2004.01059.x

Bakonyi G, Nagy P (2000) Temperature- and moisture-induced changes in the structure of the nematode fauna of a semiarid grassland-patterns and mechanisms. Glob Change Biol 6:697–707

Bardgett RD, Chan KF (1999) Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in montane grassland ecosystems. Soil Biol Biochem 31:1007–1014

Bardgett RD, Whittaker JB, Frankland JC (1993) The diet and food preferences of *Onychiurus procampatus* (Collembola) from upland grassland soils. Biol Fert Soils 16:296–298

Barker DH, Vanier C, Naumburg E, Charlet TN, Nielsen KM, Newingham BA, Smith SD (2006) Enhanced monsoon precipitation and nitrogen deposition affect leaf traits and photosynthesis differently in spring and summer in the desert shrub *Larrea tridentate*. New Phytol 169:799–808

Beare MH, Coleman DC, Crossley DA, Hendrix PF, Odum EP (1995) A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant Soil 170:5–22

Bokhorst S, Huikes A, Convey P, van Bodegom PM, Aerts R (2008) Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. Soil Biol Biochem 40:1547–1556

Bouwman LA, Zwart KB (1994) The ecology of bacterivorous protozoans and nematodes in arable soil. Agric Ecosyst Environ 51:145–160

Bradford MA, Tordoff GM, Eggers T, Jones TH, Newington JE (2002a) *Microbiota*, fauna, and mesh size interactions in litter decomposition. Oikos 99:317–323

Bradford MA, Jones TH, Bardgett RD et al (2002b) Impacts of soil faunal community composition on model grassland ecosystems. Science 298:615–618

Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecol Lett 11:1316–1327

Briones MJI, Ineson P, Sleep D (1999) Use of $\delta^{13}C$ to determine food selection in collembolan species. Soil Biol Biochem 31:937–940

Briones MJI, Ineson P, Heinemeyer A (2007) Predicting potential impacts of climate change on the geographical distribution of enchytraeids: a meta-analysis approach. Glob Change Biol 13:2252–2269

Briones MJI, Ostle NJ, McNamara NP, Poskitt J (2009) Functional shifts of grassland soil communities in response to soil warming. Soil Biol Biochem 41:315–322

Brussaard L (1998) Soil fauna, guilds, functional groups and ecosystem processes. Appl Soil Ecol 9:123–135

Brussaard L, Behan-Pelletier VM, Bignell DE et al (1997) Biodiversity and ecosystem functioning in soil. Ambio 26:563–570

Bushby HVA, Marshall KC (1977) Some factors affecting the survival of root-nodule bacteria on desiccation. Soil Biol Biochem 9:143–147

Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. Science 277:500–504

Chen B, Snider RJ, Snider RM (1996) Food consumption by Collembola from northern Michigan deciduous forest. Pedobiologia 40:149–161

Clarholm M (1989) Effects of plant–bacterial–amoebal interactions on plant uptake of nitrogen under field conditions. Biol Fert Soils 8:373–378

Cole L, Bardgett RD, Ineson P, Adamson JK (2002) Relationships between enchytraeid worms (Oligochaeta), climate change, and the release of dissolved organic carbon from blanket peat in northern England. Soil Biol Biochem 34:599–607

Convey P, Wynn-Williams DD (2002) Antarctic soil nematode response to artificial climate amelioration. Eur J Soil Biol 38:255–259

Convey P, Pugh A, Jackson C, Murray AW, Ruhland CT, Xiong FS, Day TA (2002) Response of Antarctic terrestrial microarthropods to long-term climate manipulations. Ecology 83:3130–3140

Cornejo FH, Varela A, Wright SJ (1994) Tropical forest decomposition under seasonal drought: nutrient release, fungi and bacteria. Oikos 70:183–190

Coulson SJ, Hodkinson ID, Webb NR, Block W, Bale JS, Strathdee AT, Worland MR, Wooley C (1996) Effects of experimental temperature elevation on high-arctic soil microarthropod populations. Polar Biol 16:147–153

Coulson SJ, Leinaas HP, Ims RA, Søvik G (2000) Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. Ecography 23:299–306

Cragg RG, Bardgett RD (2001) How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. Soil Biol Biochem 33:2073–2081

De Graaff MA, van Groenigen KJ, Six J, Hungate B, van Kessel C (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta-analysis. Glob Change Biol 12:2077–2091

Del Grosso S, Parton W, Stohlgren T, Zheng D, Bachelet D, Prince S, Hibbard K, Olson R (2008) Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89:2117–2126

Denef K, Six J, Bossuyt H, Frey SD, Elliott ET, Merckx R, Paustian K (2001) Influence of dry-wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biol Biochem 33:1599–1611

Dermody O, Weltzin JF, Engel EC, Allen P, Norby RJ (2007) How do elevated [CO_2], warming, and reduced precipitation interact to affect soil moisture and LAI in an old field ecosystem. Plant Soil 301:255–266

Didden WAM (1993) Ecology of terrestrial Enchytraeidae. Pedobiologia 37:2–29

Drake BG, Gonzàlez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? Annu Rev Plant Phys 48:609–639

Drigo B, Kowalchuk GA, Van Veen JA (2008) Climate change goes underground: effects of elevated atmospheric CO_2 on microbial community structure and activities in the rhizosphere. Biol Fert Soils 44:667–679

Elliott ET, Anderson RV, Coleman DC, Cole CV (1980) Habitable pore space and microbial trophic interactions. Oikos 35:327–335

Field CB, Jackson RB, Mooney HA (1995) Stomatal responses to increased CO_2: implications from the plant to the global scale. Plant Cell Environ 18:1214–1225

Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777–787

Fierer N, Strickland MS, Liptzin D, Bradford MA, Cleveland CC (2009) Global patterns in belowground communities. Ecol Lett 12:1238–1249

Freckman DW, Whitford WG, Steinberger Y (1987) Effect of irrigation on nematode population dynamics and activity in desert soils. Biol Fert Soils 3:3–10

Gerten D, Luo Y, Maire Le et al (2008) Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. Glob Change Biol 14:2365–2379

Goverde M, Erhardt A, Niklaus PA (2002) In situ development of a satyrid butterfly on calcareous grassland exposed to elevated carbon dioxide. Ecology 83:1399–1411

Griffiths BS (1986) Mineralization of nitrogen and phosphorus by mixed cultures of the ciliate protozoan *Colpoda steinii*, the nematode *Rhabditis* sp. and the bacterium *Pseudomonas fluorescens*. Soil Biol Biochem 18:637–641

Gulledge J, Schimel JP (1998) Moisture control over atmospheric CH_4 consumption and CO_2 production in diverse Alaskan soils. Soil Biol Biochem 30:1127–1132

Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2010) Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. Glob Change Biol 16:2272–2286

Haimi J, Laamanen J, Penttinen R, Räty M, Koponen S, Kellomäki S, Niemelä P (2005) Impacts of elevated CO_2 and temperature on the soil fauna of boreal forests. Appl Soil Ecol 30:104–112

Hairston N, Smith F, Slobodkin L (1960) Community structure, population control, and competition. Am Nat 94:421–425

Harrington R, Woiwod I, Sparks T (1999) Climate change and trophic interactions. Trends Ecol Evol 14:146–150

Harte J, Rawa A, Price V (1996) Effects of manipulated soil microclimate on mesofaunal biomass and diversity. Soil Biol Biochem 28:313–322

Hassink J, Bouwman LA, Zwart KB, Brussaard L (1993) Relationships between habitable pore space, soil niota and mineralization rates in grassland soils. Soil Biol Biochem 25:47–55

Hattori T (1988) Soil aggregates in microhabitats of microorganisms. Rep Inst Agric Res Tohoku Univ 37:23–36

Hedlund K, Öhrn MS (2000) Tritrophic interactions in a soil community enhance decomposition rates. Oikos 88:585–591

Heemsbergen DA, Berg MP, Loreau M, van Hal JR, Faber JH, Verhoef HA (2004) Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306:1019–1020

Hendrix PF, Parmelee RW, Crossley DA, Coleman DC, Odum EP, Groffman PM (1986) Detritus food webs in conventional and no-tillage agroecosystems. Bioscience 36:374–380

Hodkinson ID, Healey V, Coulson S (1994) Moisture relationships of the high arctic collembolan *Onychiurus arcticus*. Physiol Entomol 19:109–114

Hoeksema JD, Lussenhop J, Teeri JA (2000) Soil nematodes indicate food web responses to elevated atmospheric CO_2. Pedobiologia 44:725–735

Hughes L (2000) Biological consequences of global warming: is the signal already. Trends Ecol Evol 15:56–61

Hungate BA, Jaeger CH III, Gamara G, Chapin FS III, Field CB (2000) Soil *microbiota* in two grasslands: responses to elevated atmospheric CO_2. Oecologia 124:589–598

Hungate BA, Stiling PD, Dijkstra P, Johnson DW, Ketterer ME, Hymus GI, Hinkle CR, Drake BG (2004) CO_2 elicits long-term decline in nitrogen fixation. Science 304:1291

Hungate BA, van Groenigen KJ, Six J, Jastrow JD, Luo Y, de Graaff MA, van Kessel C, Osenberg CW (2009) Assessing the effect of elevated carbon dioxide on soil carbon: a comparison of four meta-analyses. Glob Change Biol 15:2020–2034

Hunt HW, Coleman DC, Ingham ER et al (1987) The detrital food web in a shortgrass prairie. Biol Fert Soils 3:57–68

Ingham RE, Trofymow JA, Ingham ER, Coleman DC (1985) Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecol Monogr 55:119–140

Ingham ER, Trofymow JA, Ames RN, Hunt HW, Morley CR, Moore JC, Coleman DC (1986) Trophic interactions and nitrogen cycling in a semi-arid grassland soil. I. Seasonal dynamics of the natural populations, their interactions and effects on nitrogen cycling. J Appl Ecol 23:597–614

Jastrow JD, Miller RM, Matamala R, Norby RJ, Boutton TW, Rice CW, Owensby CE (2005) Elevated atmospheric carbon dioxide increases soil carbon. Glob Change Biol 11:2057–2064

Jones FGW, Larbey DW, Parrott DM (1969) The influence of soil structure and moisture on nematodes, especially *Xiphinema*, *Longidorus*, *Trichodorus* and *Heterodera* spp. Soil Biol Biochem 1:153–165

Kardol P, Reynolds WN, Norby RJ, Classen AT (2011) Climate change effects on soil microarthropod abundance and community structure. Appl Soil Ecol 47:37–44

Keith DM, Johnson EA, Valeo C (2010) Moisture cycles of the forest floor organic layer (F and H layers) during drying. Water Resour Res 46:W07529. doi:10.1029/2009WR007984

Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Glob Change Biol 10:1870–1877

Klironomos JN, Rillig MC, Allen MF (1996) Below-ground microbial and microfaunal responses to *Artemisia tridentate* grown under elevated atmospheric CO_2. Funct Ecol 10:527–534

Klironomos JN, Rillig MC, Allen MF, Zak DR, Kubiske M, Pregitzer KS (1997) Soil fungal-arthropod responses to *Populus temuloides* grown under enriched atmospheric CO_2 under field conditions. Glob Change Biol 3:473–478

Klironomos JN, Allen MF, Rillig MC, Piotrowski J, Makvandi-Nejad S, Wolfe BE, Powell JR (2005) Abrupt rise in atmospheric CO_2 overestimates community response in a model plant–soil system. Nature 433:621–624

Kuikman PJ, Van Veen JA (1989) The impact of protozoa on the availability of bacterial nitrogen to plants. Biol Fert Soils 8:13–18

Kuikman PJ, Van Vuuren MMI, Van Veen JA (1989) Effect of soil moisture regime on predation by protozoa of bacterial biomass and the release of bacterial nitrogen. Agric Ecosyst Environ 27:271–279

Laakso J, Setälä H, Palojärvi A (2000) Influence of decomposer food web structure and nitrogen availability on plant growth. Plant Soil 225:153–165

Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillion S (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. Eur J Soil Biol 33:159–193

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771

Lensing JR, Wise DH (2006) Predicted climate change alters the indirect effect of predators on an ecosystem process. Proc Natl Acad Sci USA 103:15502–15505

Lensing JR, Wise DH (2007) Impact of changes in rainfall amounts predicted by climate-change models on decomposition in a deciduous forest. Appl Soil Ecol 35:523–534

Lindberg N, Persson T (2004) Effects of long-term nutrient fertilization and irrigation on the microarthropod community in a boreal Norway spruce stand. For Ecol Manag 188:125–135

Lindberg N, Engtsson JB, Persson T (2002) Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. J Appl Ecol 39:924–936

Luo Y (2001) Transient ecosystem responses to free-air CO_2 enrichment (FACE): experimental evidence and methods of analysis. New Phytol 152:3–8

Luo Y, Wan S, Hui D, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413:622–625

Luo Y, Su B, Currie WS et al (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54:731–739

Meyer WM, Ostertag R, Cowie RH (2010) Macro-invertebrates accelerate litter decomposition and nutrient release in a Hawaiian rainforest. Soil Biol Biochem 43:206–211

Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JB, Nowak RS, Parton WJ, Polley HW, Shaw MR (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140:11–25

Neher DA, Weicht TR, Moorhead DL, Sinsabaugh RL (2004) Elevated CO_2 alters functional attributes of nematode communities in forest soils. Funct Ecol 18:584–591

Nijs I, Impens I (1996) Effects of elevated CO_2 concentration and climate-warming on photosynthesis during winter in *Lolium perenne*. J Exp Bot 47:915–924

Niklaus PA, Alphei J, Ebersberger D, Kampichler C, Kandeler E, Tscherko D (2003) Six years of in situ CO_2 enrichment evoke changes in soil structure and soil biota of nutrient-poor grassland. Glob Change Biol 9:585–600

Niu S, Li Z, Xia J, Han Y, Wu M, Wan S (2008) Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China. Environ Exp Bot 63:91–101

Norby RJ, Luo Y (2004) Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. New Phytol 162:281–293. doi:10.1111/j.1469-8137.2004.01047.x

Odhiambo HO, Ong CK, Deans JD, Wilson J, Khan AAH, Sprent JI (2001) Roots, soil water and crop yield: tree crop interactions in a semi-arid agroforestry system in Kenya. Plant Soil 235:221–233

Oren R, Ellsworth DE, Johnsen KH et al (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411:469–472

Osenberg CW, Sarnelle O, Cooper SD (1997) Effect size in ecological experiments: the application of biological models in meta-analysis. Am Nat 150:798–812

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phonological response to global warming. Glob Change Biol 13:1860–1872

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Peters RH (1993) A critique for ecology. Cambridge University Press, Cambridge

Petersen H, Luxton M (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39:288–388

Ponsard S, Arditi R (2000) What can stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) tell us about the food web of soil macro-invertebrates? Ecology 81:852–864

Prieto P, Peñuelas J, Llusià J, Asensio D, Estiarte M (2009) Effects of long-term experimental night-time warming and drought on photosynthesis, Fv/Fm and stomatal conductance in the dominant species of a Mediterranean shrubland. Acta Physiol Plant 31:729–739

Rosenberg MS, Adams DC, Gurevitch J (2000) MetaWin Version 2.1: Statistical software for meta-analysis. Sinauer, Boston

Ruess L, Michelsen A, Schmidt IK, Jonasson S (1999) Simulated climate change affecting microorganisms, nematode density and biodiversity in subarctic soils. Plant Soil 212:63–73

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562

Rutherford PM, Juma NG (1992) Influence of texture on habitable pore space and bacterial-protozoan populations in soil. Biol Fert Soils 12:221–227

Rygiewicz PT, Monleon VJ, Ingham ER, Martin KJ, Johnson MG (2010) Soil life in reconstructed ecosystems: initial soil food web responses after rebuilding a forest soil profile for a climate change experiment. Appl Soil Ecol 45:26–38

Savin MC, Görres JH, Neher DA, Amador JA (2001) Biogeophysical factors influencing soil respiration and mineral nitrogencontent in an old field soil. Soil Biol Biochem 33:429–438

Scheu S (2002) The soil food web: structure and perspectives. Eur J Soil Biol 38:11–20

Scheu S, Falca M (2000) The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123:285–296

Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB (2002) Grassland responses to global environmental changes suppressed by elevated CO_2. Science 298:1987–1990

Shi L, Guttenberger M, Kottke I, Hampp R (2002) The effect of drought on mycorrhizas of beech (*Fagus sylvatica* L.): changes in community structure, and the content of carbohydrates and nitrogen storage bodies of fungi. Mycorrhiza 12:303–311

Sinclair BJ (2002) Effect of increased temperatures simulating climate change on terrestrial invertebrates on Ross Island, Antarctica. Pedobiologia 46:150–160

Six J, Carpentier A, van Kessel C, Merckx, Harris D, Horwath WR, Lüscher A (2001) Impact of elevated CO_2 on soil organic matter dynamics as related to changes in aggregate turnover and residue quality. Plant Soil 234:27–36

Six J, Frey SD, Thiet RK, Batten KM (2006) Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Sci Soc Am J 70:555–569

Sjursen H, Michelsen A, Holmstrup M (2005) Effects of freeze-thaw cycles on microarthropods and nutrient availability in a sub-Arctic soil. Appl Soil Ecol 28:79–93

Sonnemann I, Wolters V (2005) The microfood web of grassland soils responds to a moderate increase in atmospheric CO_2. Glob Change Biol 11:1148–1155

Sowerby A, Emmett B, Beier C, Tietema A, Peñuelas J, Estiarte M, Van Meeteren MJM, Hughes S, Freeman C (2005) Microbial community changes in heathland soil communities along a geographical gradient: interaction with climate change manipulations. Soil Biol Biochem 37:1805–1813

Staddon PL, Fitter AH (1998) Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? Trends Ecol Evol 13:455–458

Stiling P, Cornelissen T (2007) How does elevated carbon dioxide (CO_2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. Glob Change Biol 13:1823–1842

Strickland MS, Rousk J (2010) Considering fungal:bacterial dominance in soils–methods, controls, and ecosystem implications. Soil Biol Biochem 42:1385–1395

Strong DT, De Wever H, Merckx R, Recous S (2004) Spatial location of carbon decomposition in the soil pore system. Eur J Soil Sci 55:739–750

Todd TC, Blair JM, Milliken GA (1999) Effects of altered soil–water availability on a tallgrass prairie nematode community. Appl Soil Ecol 13:45–55

Treseder KK (2004) A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol 164:347–355

Tsiafouli MA, Kallimanis AS, Katana E, Stamou GP, Sgardelis SP (2005) Responses of soil microarthropods to experimental short-term manipulations of soil moisture. Appl Soil Ecol 29:17–26

Van Gestel M, Merckx R, Vlassak K (1996) Spatial distribution of microbial biomass in microaggregates of a silty-loam soil and the relation with the resistance of microorganisms to soil drying. Soil Biol Biochem 28:503–510

Van Veen JA, Paul EA (1979) Conversion of biovolume measurements of soil organisms, grown under various moisture tensions, to biomass and their nutrient content. Appl Environ Microbiol 37:686–692

Van Vliet PCJ, Beare MH, Coleman DC (1995) Population dynamics and functional roles of Enchytraeidae (Oligochaeta) in hardwood forest and agricultural ecosystems. Plant Soil 170:199–207

Vargas R, Hattori T (1986) Protozoan predation of bacterial cells in soil aggregates. FEMS Microbiol Ecol 38:233–242

Verhoef HA, Brussaard L (1990) Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. Biogeochemistry 11:175–211

Wall DH, Bradford MA, St. John MG et al (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Glob Change Biol 14:2661–2677

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton

Weltzin JF, Loik ME, Schwinning S et al (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53:941–952

West AW, Sparling GP, Speir TW, Wood JM (1988) Dynamics of microbial-C, N-flush and ATP, and enzyme activities of gradually dried soils from a chronosequence. Aust J Soil Res 26:519–530

West AW, Sparling GP, Feltham CW, Reynolds J (1992) Microbial activity and survival in soil dried at different rates. Aust J Soil Res 30:209–222

Woods LE, Cole CV, Elliott ET, Anderson RV, Coleman DC (1982) Nitrogen transformations as affected by bacterial–microfaunal interactions. Soil Biol Biochem 14:93–98

Wright SF, Upadhyaya A (1998) A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant Soil 198:97–107

Wright DA, Killham K, Glover LA, Prosser JI (1995) Role of pore size location in determining bacterial activity during predation by Protozoa in soil. Appl Environ Microbiol 61:3537–3543

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2010) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob Change Biol. doi:10.1111/j.1365-2486.2010.02302.x

Yeates GW, Bongers T, de Goede RG, Freckman DW, Georgieva SS (1993) Feeding habits in soil nematode families and genera—an outline for soil ecologists. J Nematol 25:315–331

Yeates GW, Tate KR, Newton PCD (1997) Response of the fauna of a grassland soil to doubling of atmospheric carbon dioxide concentration. Biol Fert Soils 25:307–315

Yeates GW, Newton PCD, Ross DJ (2003) Significant changes in soil microfauna in grazed pasture under elevated carbon dioxide. Biol Fert Soils 38:319–326

Zak DR, Pregitzer KS, King JS, Holmes WE (2000) Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: a review and hypothesis. New Phytol 147:201–222

Zogg GP, Zak DR, Ringelberg DB, MacDonald NW, Pregitzer KS, White DC (1997) Compositional and functional shifts in microbial communities due to soil warming. Soil Sci Soc Am J 61:475–481