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# Climate change effects on soil microarthropod abundance and community structure

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ABSTRACT

Long-term ecosystem responses to climate change strongly depend on how the soil subsystem and its inhabitants respond to these perturbations. Using open-top chambers, we studied the response of soil microarthropods to single and combined effects of ambient and elevated atmospheric [$CO_2$], ambient and elevated temperatures and changes in precipitation in constructed old-fields in Tennessee, USA. Microarthropods were assessed five years after treatments were initiated and samples were collected in both November and June. Across treatments, mites and collembola were the most dominant microarthropod groups collected.

We did not detect any treatment effects on microarthropod abundance. In November, but not in June, microarthropod richness, however, was affected by the climate change treatments. In November, total microarthropod richness was lower in dry than in wet treatments, and in ambient temperature treatments, richness was higher under elevated [$CO_2$] than under ambient [$CO_2$]. Differential responses of individual taxa to the climate change treatments resulted in shifts in community composition. In general, the precipitation and warming treatments explained most of the variation in community composition. Across treatments, we found that collembola abundance and richness were positively related to soil moisture content, and that negative relationships between collembola abundance and richness and soil temperature could be explained by temperature-related shifts in soil moisture content.

Our data demonstrate how simultaneously acting climate change factors can affect the structure of soil microarthropod communities in old-field ecosystems. Overall, changes in soil moisture content, either as direct effect of changes in precipitation or as indirect effect of warming or elevated [$CO_2$], had a larger impact on microarthropod communities than did the direct effects of the warming and elevated [$CO_2$] treatments. Moisture-induced shifts in soil microarthropod abundance and community composition may have important impacts on ecosystem functions, such as decomposition, under future climatic change.

## 1. Introduction

Atmospheric $CO_2$ concentrations ([$CO_2$]) are rising, resulting in increases in global atmospheric temperatures (2.0–4.5 °C by the year 2100), and modification of precipitation patterns (IPCC, 2007). Long-term ecosystem responses to atmospheric and climatic changes (hereafter 'climate changes') may largely depend on how the soil subsystem responds to these perturbations (e.g., Davidson and Janssens, 2006; Bardgett et al., 2008). While recent studies have focused on how climate changes can impact soil microbial communities and the ecosystem processes that they control, such as litter decomposition and nutrient cycling (e.g., Bardgett et al., 2008; Castro et al., 2010; Kardol et al., 2010b), effects of climate changes on soil microarthropods received less attention (Hågvar and Klanderud, 2009). Soil microarthropods play an important role in the functioning of the decomposer food web by, for example, exerting top-down control of primary (bacteria, fungi) and secondary (nematodes, protozoa) decomposers (e.g., Petersen and Luxton, 1982; Seastedt, 1984; Beare et al., 1992; Cole et al., 2004; Filser, 2002; Sackett et al., 2010). Soil microarthropods also affect decomposition processes directly through fragmentation of litter and through fecal production (e.g., Seastedt, 1984; Sackett et al., 2010). Hence, a better understanding of effects of climate changes on the abundance and community structure of soil microarthropods can aid predictions of how soil ecosystems may function under future climatic conditions.

Climate changes can influence soil microarthropod community abundance and composition directly by altering soil microclimate and indirectly by altering resource availability and the composition of the soil food web. Warming and changes in precipitation

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amounts, for example, can directly alter soil temperature and moisture, factors that strongly influence microarthropod reproduction and development rates (e.g., van Straalen, 1994; Uvarov, 2003). In fact, soil microarthropods are extremely responsive to changes in soil moisture, a pattern seen in numerous studies across diverse ecosystems (e.g., Frampton et al., 2000; Pflug and Wolters, 2001; Lindberg et al., 2002; Tsiafouli et al., 2005; Moron-Rios et al., 2010). Unlike soil moisture, warming impacts on microarthropods have been context dependent and abundance responses varied across experiments (e.g., Coulson et al., 1996; Huhta and Hänninen, 2001; Hågvar and Klanderud, 2009). Work by Sjursen et al. (2005) suggested that warming may indirectly alter soil microarthropod communities by causing a shift in the abundance and composition of soil organisms upon which they prey. In addition, temperature and other climate factors may indirectly influence soil microarthropod communities through changes in plant physiology or community structure which can alter resource availability and microhabitat conditions (e.g., Cotrufo and Ineson, 1995; Kardol et al., 2010b).

The limited number of studies on response of soil microarthropods to climate change have often focused on single-factor effects of elevated [$CO_2$] (e.g., Jones et al., 1998; Lussenhop et al., 1998; Hansen et al., 2001), warming (e.g., Coulson et al., 1996; Bokhorst et al., 2008), or changes in precipitation patterns (e.g., O'Lear and Blair, 1999; Tsiafouli et al., 2005). Climate changes, however, will not happen in isolation of one another. For example, elevated [$CO_2$] may ameliorate negative effects of soil drying through reducing plant stomatal conductance and transpiration, while increased evapotranspiration resulting from higher temperatures may exacerbate effects of soil drying (e.g., Dermody et al., 2007). On the other hand, drying may result in more extreme soil temperatures (e.g., Tsiafouli et al., 2005). Interactions among climate change variables, thus may alter soil microarthropod communities in ways that are not always predictable from the impact of individual climate change factors (Couteaux and Bolger, 2000; Loranger et al., 2004). For example, Harte et al. (1996) found that warming increased microarthropod abundance and biomass under wet conditions, but not under dry conditions.

We took advantage of a long-term, multi-factor climate change experiment in constructed old-field ecosystems (established in 2002) to investigate the single and interactive effects of atmospheric [$CO_2$], air temperature, and precipitation on soil microarthropod abundance and community structure. We measured treatment responses of soil microarthropods at two different sampling points, one at the end of the growing season and one at the end of the experiment (November 2007 and June 2008, respectively). Each of the climate change factors has the potential to affect soil microarthropods; however, because microarthropods are sensitive to soil drying, we predicted that the dry treatment would have the strongest effect on microarthropod abundance and community structure. Because [$CO_2$] and temperature can both alter soil moisture (directly or indirectly via changes in plant physiology and plant community structure), we also predicted there would be interactive effects of precipitation, [$CO_2$], and temperature on microarthropod communities.

## 2. Materials and methods

### 2.1. Experimental design

The Old field Community, Climatic and Atmospheric Manipulation (OCCAM) experiment was established at Oak Ridge National Environmental Research Park (35° 54′ N; 84° 21′ W) in Oak Ridge, Tennessee, USA. The site was used for agriculture until 1943 and then was left fallow until 1964 when a managed fescue field was established. Soils are classified as Captina silt loam – fine-silty, siliceous, mesic typic fragiudult, well drained, and slightly acidic (Edwards and Norby, 1999). Whole-soil N ($1.62\,g\,N\,kg^{-1}$) and C ($18.3\,g\,C\,kg^{-1}$), determined prior to the start of the experiment, were not affected by the climate change treatments and did not change over time (Garten et al., 2009). Experimental plots were established in 2002 and were planted with seven plant species common to old fields in the southeastern United States—*Plantago lanceolata* L., a herbaceous forb; *Andropogon virginicus* L., a cespitose $C_4$ bunchgrass; *Festuca pratense* L. syn *F. elatior* L., a $C_3$ bunchgrass; *Dactylis glomerata* L., a $C_3$ bunchgrass; *Trifolium pratense* L., a herbaceous legume; *Solidago canadensis*, a herbaceous forb; and *Lespedeza cuneata*, a $N_2$-fixing sub-shrub. The response of the plant community over time is described in Engel et al. (2009) and in Kardol et al. (2010a). The experimental design is described in detail elsewhere (Wan et al., 2007; Dermody et al., 2007; Garten et al., 2008). Briefly, in 2003, [$CO_2$], temperature, and precipitation treatments were applied using open-top chambers (4 m diameter) arranged in a randomized complete block, split-plot design ($n = 3$). Temperature and [$CO_2$] concentrations were regulated continuously starting in April 2003 with heating and cooling units and $CO_2$ additions as described in Norby et al. (1997). Rainout shelters were constructed to eliminate natural precipitation. Whole chambers were treated with ambient or elevated [$CO_2$] (ambient + 300 ppm), and ambient or elevated temperatures (ambient + 3 °C). Each chamber was split into wet and dry sub-plots, established with differential irrigation. Wet and dry plots were irrigated with weekly additions of 2 mm (dry) and 25 mm (wet) rainwater, which was collected and stored on site.

Soil volumetric water content (VWC) integrated over 0–15 cm depth was measured weekly within each sub-plot by time domain reflectometry (TDR100, Campbell Scientific) as described by Dermody et al. (2007). Averaged from October 2005 (two years prior to the date we collected our first set of soil samples; see paragraph 2.2) to June 2008 (the time we collected our second set of soil samples), within each plot, the dry sub-plots had significantly lower (3.9%) soil moisture than the wet sub-plots (Fig. 1A). Further, elevated temperature generally reduced soil moisture, while elevated [$CO_2$] generally increased soil moisture (see also Dermody et al., 2007). Changes in soil moisture in response to [$CO_2$] and temperature were small relative to the changes in soil moisture due to the precipitation treatment. Soil temperature (0–10 cm) within each sub-plot was recorded every hour using a data logger system (CR10X, Campbell Scientific). From October 2005 to June 2008, soil temperature was, on average, 1.4 °C higher in chambers with elevated temperature than in chambers with ambient temperature (ANOVA: $F_{1,6} = 59.62$, $P < 0.001$; Fig. 1B); no other treatments affected soil temperature.

### 2.2. Soil sampling and microarthropod extractions

In November 2007 and June 2008 (hereafter referred to as November and June), three soil cores (0–15 cm depth, 2 cm diameter) were collected from each sub-plot. Microarthropods were extracted from the soil samples using modified high-gradient Tullgren funnels (Crossley and Blair, 1991) for 72 h at room temperature. Individuals were collected into vials containing 70% ethanol for preservation and storage. Except for Prostigmata, mites and collembola were identified to species or morphospecies according to Christiansen and Bellinger (1980–1981), Balogh and Balogh (1992), and Niedbala (2002). Other microarthropods were identified to higher-level taxonomic groups. Juveniles were not included in the analyses. The three samples from each sub-plot were averaged to one; in our analyses, we only used one data point for each sub-plot.

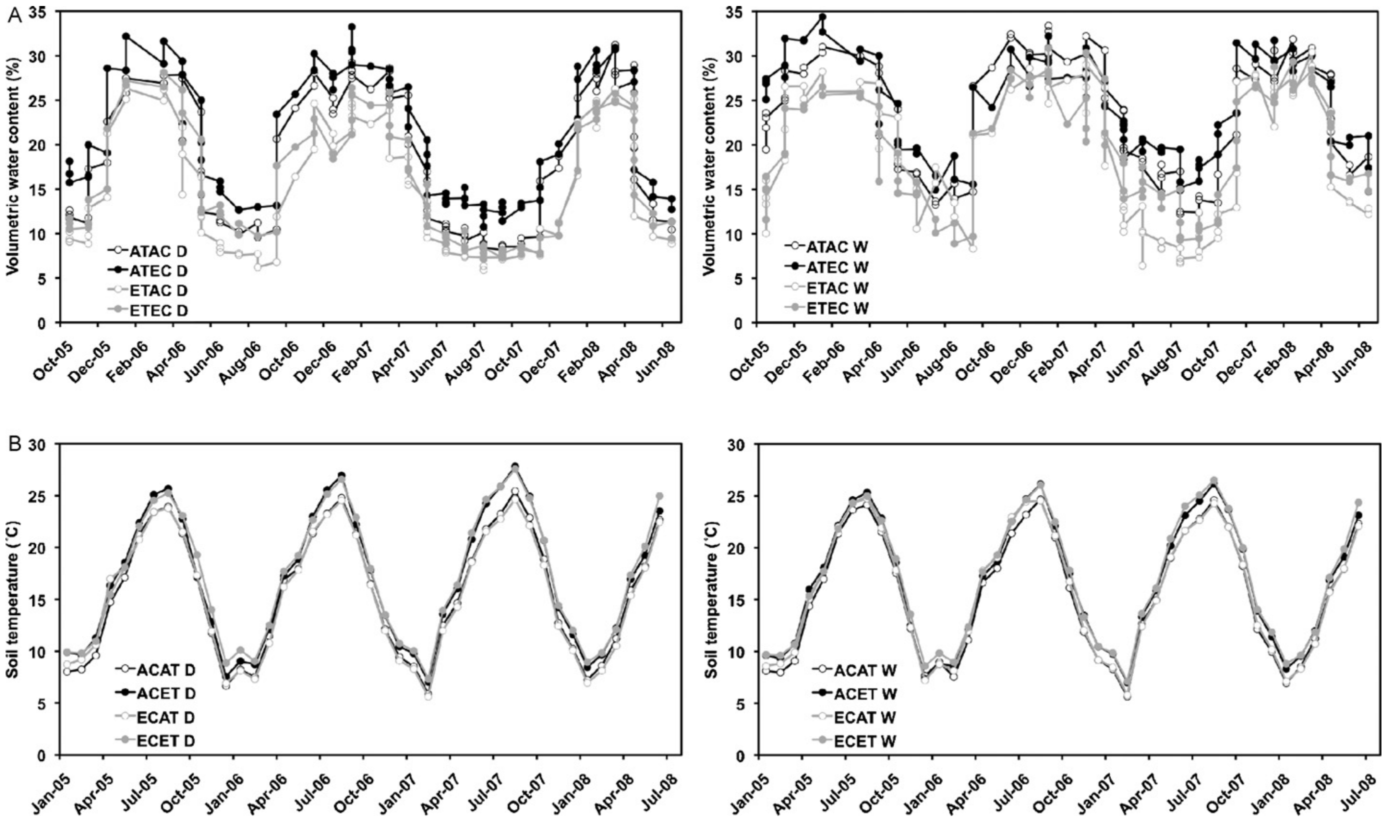

**Fig. 1.** Mean soil moisture expressed as volumetric water content (VWC) (0–15 cm) (A), and mean soil temperature (0–10 cm) (B) from October 2005 to June 2008 for precipitation, [$CO_2$], and temperature treatments. Earlier data on soil moisture in this experiment are published in Dermody et al. (2007). Each point represents the bi-monthly (two week) average for a treatment plot. Dry treatments are shown in the left panels; wet treatments are shown in the right panels. AT = ambient temperature; ET = elevated temperature; AC = ambient [$CO_2$]; EC = elevated [$CO_2$]; D = dry; W = wet.

### 2.3. *Statistical analyses*

Across treatments, microarthropod abundance and richness was significantly higher in June than in November (Fig. 2; Supplementary material, Table S1). We therefore decided to run further statistical analyses separately for the two sampling times. The direct and interactive effects of precipitation, [$CO_2$], and temperature on abundance and taxon richness (total microarthropods, and separately for mites and collembola) were tested using a three-way, split-plot analysis of variance (ANOVA) (PROC MIXED, SAS Institute, Cary, NC, USA). Precipitation, [$CO_2$], temperature, and their interactions were considered fixed effects, and blocks and the interactions between block, [$CO_2$], and temperature were included as random factors. The Kenward–Rogers method was used to estimate the denominator degrees of freedom for tests of individual fixed effects, as appropriate for data sets with small sample sizes. For abundance, data were log-transformed to meet assumptions of normality and homogeneity of variance.

Treatment effects on microarthropod community composition were analyzed using CANOCO, version 4.5 (ter Braak and Šmilauer, 2002). For the November data, the largest gradient length of detrended correspondence analysis was 3.8 standard deviation units, while for the June data, the largest gradient length was 2.9. Taken together, redundancy analysis (RDA) (i.e., a linear ordination method) was therefore considered most appropriate (Lepš and Šmilauer, 2003). RDA analyses were carried out using abundance data, and we included the climate treatments and their interactions as explanatory variables. In all RDA analyses, block was included as covariable. Significance of effects was tested using Monte Carlo permutation tests (999 permutations). To exclude variation among blocks from the statistical tests, samples were permuted within blocks. Marginal effects (i.e., the independent effect of each variable) were tested by manual selection of each individual variable.

The relationship between soil moisture/temperature and microarthropod abundance and richness (total, and separately for mites and collembola) was determined by linear regression analysis. Given the generally slow response of microarthropod populations to changes in environmental conditions (life cycles may vary from a few weeks to over two years; Walter and Proctor, 1999) and given the potential variability among groups of microarthropods in the time needed to adjust to altered soil moisture and temperature levels, we tested relationship between soil moisture/temperature and microarthropod abundance and richness using: (1) average soil moisture and temperature data at the day closest to sampling, (2) average soil moisture and temperature one month prior to the sampling day, (3) average soil moisture and temperature one year prior to the sampling day, and (4) average soil moisture and temperature two years prior to the sampling day. Average soil moisture and temperature data provide an integrated estimate of how soil microclimate might influence the abundance and diversity of microarthropods. Results from regression analyses did not differ qualitatively among the estimates of soil moisture and temperature; therefore we arbitrarily chose to only present result of analyses with average soil moisture and temperature one month prior to sampling. Soil moisture content was inversely related to soil temperature ($p < 0.01$). Therefore, we used partial least square regressions to test if significant relationships between soil temperature and microarthropod abundance and richness hold when soil moisture was corrected for. Regression analyses were run in JMP 8.0.2.2 (SAS Institute, Cary, NC, USA).

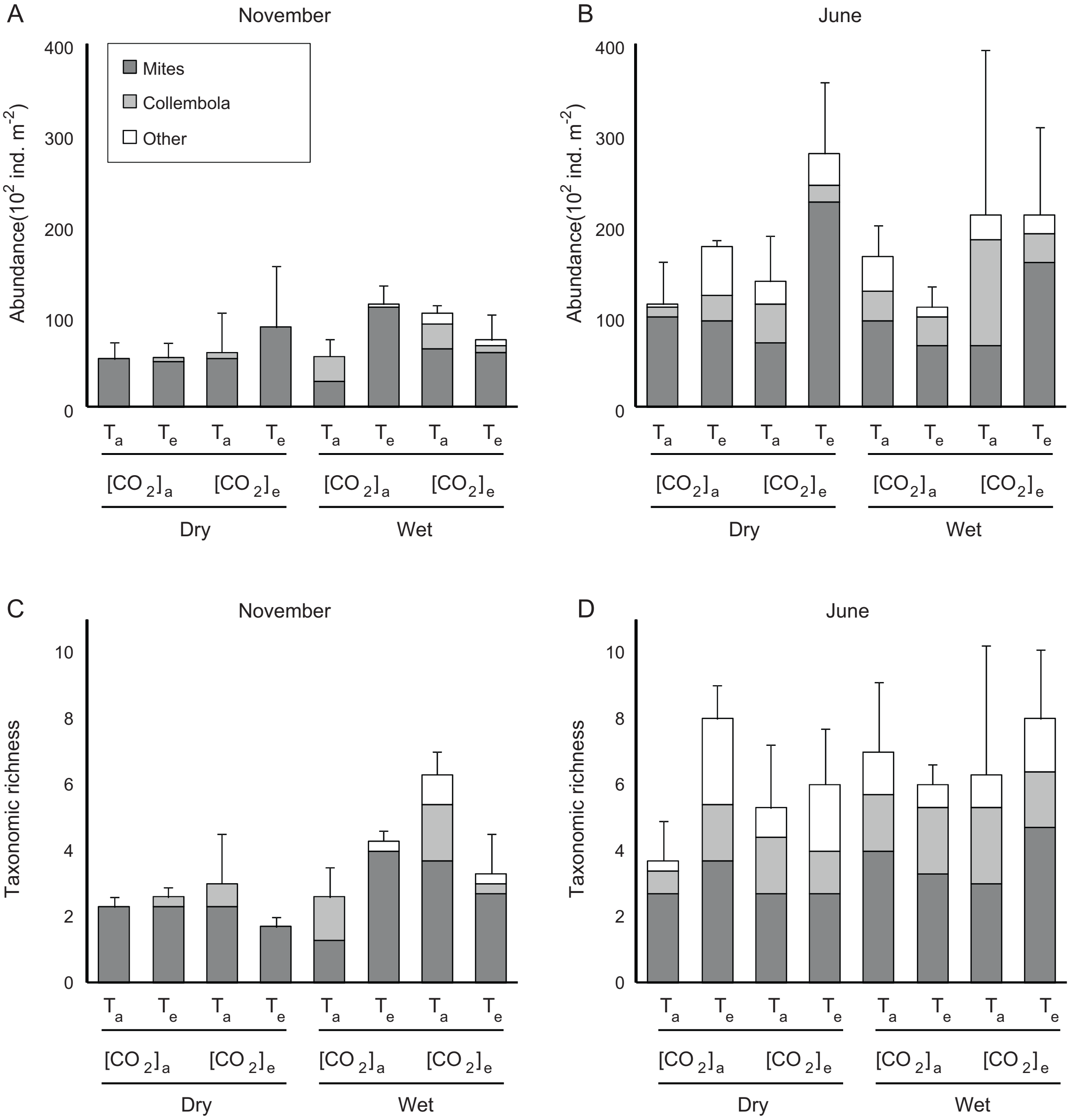

**Fig. 2.** Microarthropod abundance (A and B) and taxonomic richness (C and D) under $[CO_2]$, temperature ($T$), and precipitation treatments in November 2007 and June 2008. Data are mean ± s.e. Abbreviations: $T_a$ = ambient temperature; $T_e$ = elevated temperature; $[CO_2]_a$ = ambient $[CO_2]$; $[CO_2]_e$ = elevated $[CO_2]$.

## 3. Results

### 3.1. Microarthropod abundance and richness

Across samples, the microarthropods collected represented 34 unique taxa (Supplementary material, Table S2). Low taxonomic richness could be due to disturbances such as plot construction and plant manipulation at the beginning of the experiment. Mites were the most common group found across all the samples, followed by collembola. Other groups (Thysanoptera, Diplura, Symphyla, and Protura) were rare and not observed in all samples; therefore, they were not individually analyzed. Total microarthropod abundance and richness were generally higher in June (close to the peak of the growing season) than in November (at the end of the growing season).

We were unable to detect a difference in total microarthropod abundance, abundance of mites, and abundance of collembola across our treatments on any date (Fig. 2; Table 1). Collembola abundance was generally lower in dry than in wet treatments, but within-treatment variation was high. In contrast to the abundance data, our treatments significantly altered total microarthropod richness (Fig. 2; Table 1). In November, total microarthropod richness was lower in dry treatments than in wet treatments. Additionally, there was a significant interaction between the $[CO_2]$ and the temperature treatments: microarthropod richness was higher in treatments with elevated $[CO_2]$ than in treatments with ambient $[CO_2]$, but only under ambient temperature (Fig. 2). In June, microarthropod richness was not affected by the climate change treatments. In both seasons, richness patterns of mites and collembola generally mirrored the patterns of the total microarthropod community; however, no significant treatment effects were detected for either of these groups (Table 1).

### 3.2. Microarthropod community composition

The climate change treatments altered the compositional structure of the microarthropod community (Fig. 3; Supplementary material, Table S3). The full RDA model, including precipitation,

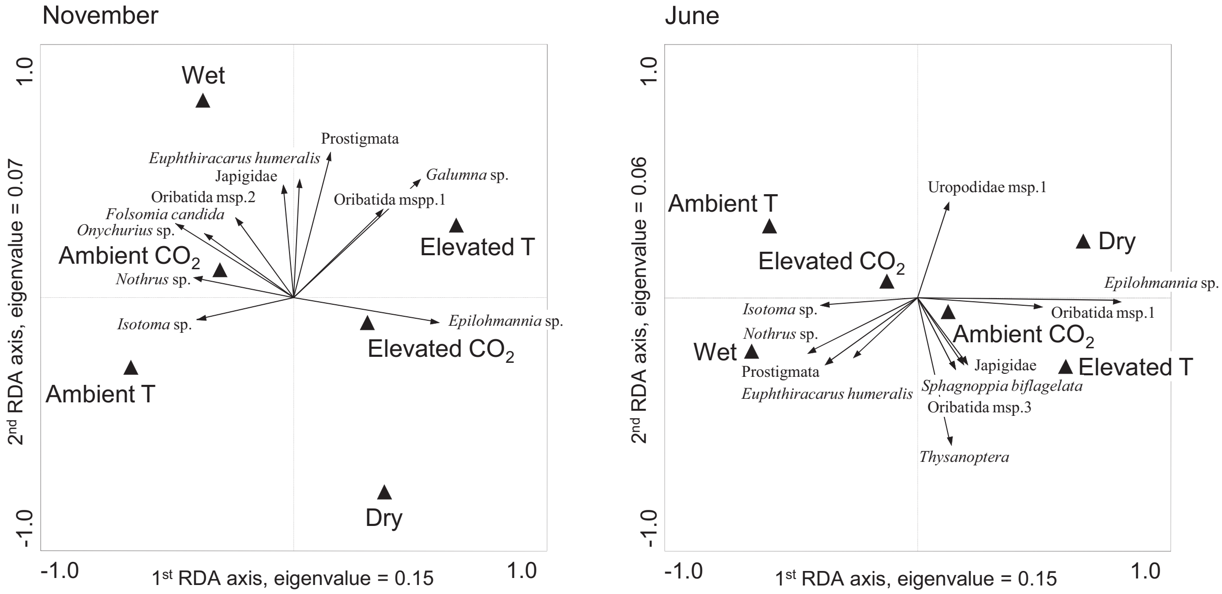

**Fig. 3.** 'Species'-treatment plots resulting from redundancy analysis showing composition of the microarthropod community in November (left) in June (right). Treatments include precipitation, [$CO_2$], temperature, and their interactions. For clarity, treatment interactions are not shown. Eigenvalues along the axes indicate the amount of explained variability in community composition. Only the best fitting taxa are shown (species fit >9% for November, and >7% for June).

[$CO_2$], and temperature as explanatory factors, explained 32% and 33% of the variation in community composition in November and June, respectively. In November, a significant amount of the variation in the mite community composition (8.2%) was explained by the temperature treatment, as shown on the first RDA axis (Fig. 3). The remaining treatments did not explain a significant amount of the variation. However, most taxa were positively associated with wet treatments, and most strongly under ambient [$CO_2$] (as indicated by the marginally significant interaction between water and [$CO_2$]; Supplementary material, Table S3). In June, variation in microarthropod community composition was significantly explained by precipitation (12.8%), temperature (10.7%), and the interaction between [$CO_2$] and temperature (15.5%) (Supplementary material, Table S3). Most notably, the oribatid mite *Epilohmannia* sp. was strongly associated with dry treatments, and with elevated temperature.

### *3.3. Relationships between soil microclimate and microarthropod abundance and richness*

In November, across treatments, there was a positive relationship between soil moisture and total microarthropod richness, but not between soil moisture and total microarthropod abundance (Table 2). There were no relationships between soil temperature and total microarthropod abundance and richness. There were positive relationships between both collembola abundance and collembola richness and soil moisture content. For collembola, there were negative relationships between soil temperature and abundance, and between soil temperature and richness, however, these relationships did not hold when we controlled for soil moisture (Table 2). For mites, there was no significant relationship between abundance and richness and soil moisture content.

In June, there were no relationships between soil moisture content and any of the measured microarthropod parameters. In contrast, there was a positive relationship between soil temperature and abundance of mites; this relationship held even when soil moisture was controlled for (Table 2).

## 4. Discussion

There is increasing recognition that climate changes can affect soil organisms and the functions they provide (e.g., Schröter et al., 2004; Hågvar and Klanderud, 2009; Kardol et al., 2010b; Lindroth, 2010). Our results demonstrate that single and combined effects of elevated [$CO_2$], warming, and change in precipitation regime can shape the abundance and community structure of soil microarthropods, which are important regulators of ecosystem processes. Further, we found that climate change effects on soil microarthropods varied by sampling date, and importantly, that the major taxonomic groups of soil microarthropods, i.e., collembola and mites, differed in their response to our climate change treatments.

We found weak support for our hypothesis that the precipitation treatment would have the strongest impact on the abundance and community structure of soil microarthropods. Total microarthropod abundance was not affected by the precipitation treatment, and this could be largely attributed to the lack of response of the mites, the most abundant group of microarthropods found in our system. While positive relationships between mite abundance and soil moisture have been established across a range of ecosystems (e.g., Lindberg et al., 2002; Badejo and Akinwole, 2006; Chikoski et al., 2006; Classen et al., 2006), mites might be adapted to strong seasonal fluctuations in soil moisture content typical in old-field ecosystems in the southeastern USA. Hence, the relatively small difference in soil moisture content between wet and dry treatments may have been insufficient to cause major shifts in mite abundance. Harte et al. (1996) suggest that summer minimum water content may be more critical for mite abundance than the across-year average. While summer moisture levels in our experiment may have been critically low (5–10%), the summer minima did not differ substantially between wet and dry treatments (Fig. 1A).

While mite abundance was not responsive to our precipitation treatments, the abundance of collembola was. Collembola abundance tended to be lower in dry than in wet treatments and it was positively related to soil moisture in the November collection. However, in June, there was no relationship between soil moisture content and collembola abundance. This discrepancy between the

**Table 1**
Result from ANOVA testing the effects of climate change treatments on abundance and richness of total microarthropods, mites, and collembola in November 2007 and June 2008. df = denominator degrees of freedom, as estimated by the Kenward–Rogers method, which determines df for each variable dependent on the covariance structure related to the random effects. Bold values indicate $p \leq 0.05$.

| | | Microarthropods (total) | | | | | | Mites | | | | | | Collembola | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | November | | | June | | | November | | | June | | | November | | | June | | |
| | | df | *F* | *p* | df | *F* | *p* | df | *F* | *p* | df | *F* | *p* | df | *F* | *p* | Df | *F* | *p* |
| Abundance | Precipitation | 16 | 2.40 | 0.14 | 8 | 4.06 | 0.08 | 14 | 0.36 | 0.56 | 16 | 2.40 | 0.14 | 8 | 4.26 | 0.07 | 14 | 0.43 | 0.52 |
| | $[CO_2]$ | 16 | 0.00 | 0.96 | 8 | 0.35 | 0.57 | 14 | 0.01 | 0.91 | 16 | 0.00 | 0.96 | 8 | 0.32 | 0.59 | 14 | 0.04 | 0.85 |
| | Temperature | 16 | 0.23 | 0.64 | 8 | 2.31 | 0.17 | 14 | 1.57 | 0.23 | 16 | 0.23 | 0.64 | 8 | 2.44 | 0.16 | 14 | 1.61 | 0.23 |
| | Precipitation × $[CO_2]$ | 16 | 0.06 | 0.81 | 8 | 0.23 | 0.64 | 14 | 0.02 | 0.89 | 16 | 0.06 | 0.81 | 8 | 0.19 | 0.68 | 14 | 0.12 | 0.73 |
| | Precipitation × temperature | 16 | 0.00 | 0.97 | 8 | 2.93 | 0.13 | 14 | 0.55 | 0.47 | 16 | 0.00 | 0.97 | 8 | 3.05 | 0.11 | 14 | 0.55 | 0.47 |
| | $[CO_2]$ × temperature | 16 | 0.60 | 0.45 | 8 | 0.13 | 0.73 | 14 | 0.89 | 0.36 | 16 | 0.60 | 0.45 | 8 | 0.11 | 0.75 | 14 | 1.00 | 0.33 |
| | Precipitation × $[CO_2]$ × temperature | 16 | 1.38 | 0.26 | 8 | 1.16 | 0.31 | 14 | 2.57 | 0.13 | 16 | 1.38 | 0.26 | 8 | 0.95 | 0.36 | 14 | 2.71 | 0.12 |
| Richness | Precipitation | 16 | **9.88** | **0.01** | 8 | 2.22 | 0.17 | 16 | 3.03 | 0.10 | 14 | 3.91 | 0.07 | 8 | 4.08 | 0.08 | 6 | 1.48 | 0.26 |
| | $[CO_2]$ | 16 | 1.31 | 0.27 | 6 | 0.02 | 0.88 | 16 | 0.12 | 0.73 | 14 | 0.16 | 0.70 | 8 | 0.32 | 0.59 | 6 | 0.07 | 0.80 |
| | Temperature | 16 | 1.31 | 0.27 | 6 | 0.78 | 0.41 | 16 | 0.12 | 0.73 | 14 | 1.41 | 0.26 | 8 | 2.89 | 0.13 | 6 | 0.01 | 0.93 |
| | Precipitation × $[CO_2]$ | 16 | 1.31 | 0.27 | 8 | 0.33 | 0.58 | 16 | 0.48 | 0.50 | 14 | 0.63 | 0.44 | 8 | 0.08 | 0.78 | 6 | 0.03 | 0.87 |
| | Precipitation × temperature | 16 | 0.00 | 1.00 | 8 | 2.22 | 0.17 | 16 | 1.94 | 0.18 | 14 | 0.00 | 1.00 | 8 | 4.08 | 0.08 | 6 | 0.27 | 0.62 |
| | $[CO_2]$ × temperature | 16 | **6.61** | **0.02** | 6 | 0.02 | 0.88 | 16 | 4.36 | 0.05 | 14 | 0.63 | 0.44 | 8 | 0.32 | 0.59 | 6 | 0.38 | 0.56 |
| | Precipitation × $[CO_2]$ × temperature | 16 | 2.04 | 0.17 | 8 | 4.75 | 0.06 | 16 | 3.03 | 0.10 | 14 | 3.91 | 0.07 | 8 | 0.75 | 0.41 | 6 | 0.03 | 0.87 |

**Table 2**
Relationship between soil moisture content (average one month prior to soil sampling) and soil microarthropod abundance and richness across climate change treatments. Data are shown for November 2007 and June 2008.

| | | Soil moisture | | | | | | | | Soil temperature | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | November | | | | June | | | | November | | | | June | | | |
| | | $R^2$ | Sign | $F_{1,22}$ | *p* | $R^2$ | Sign | $F_{1,22}$ | *p* | $R^2$ | Sign | $F_{1,22}$ | *p* | $R^2$ | Sign | $F_{1,22}$ | *p* |
| Abundance | Total microarthropods | 0.02 | – | 0.44 | 0.52 | 0.02 | – | 0.52 | 0.48 | 0.01 | + | 0.17 | 0.69 | 0.14 | + | 3.63 | 0.07 |
| | Mites | 0.02 | – | 0.44 | 0.51 | 0.09 | – | 2.06 | 0.16 | 0.07 | + | 1.56 | 0.22 | 0.35 | + | **12.06** | **<0.01** |
| | Collembola | **0.37** | **+** | **13.13** | **<0.01** | 0.01 | + | 0.18 | 0.67 | **0.20** | – | **5.53** | **0.03**[a] | 0.00 | – | 0.01 | 0.94 |
| Richness | Total microarthropods | **0.32** | **+** | **10.17** | **<0.01** | 0.01 | – | 0.23 | 0.63 | 0.09 | – | 2.30 | 0.14 | 0.06 | + | 1.32 | 0.26 |
| | Mites | 0.02 | + | 0.51 | 0.48 | 0.00 | + | 0.06 | 0.81 | 0.00 | – | 0.06 | 0.82 | 0.06 | + | 1.51 | 0.23 |
| | Collembola | **0.38** | **+** | **13.55** | **<0.01** | 0.01 | – | 0.14 | 0.71 | **0.19** | – | **5.09** | **0.03**[a] | 0.01 | + | 0.15 | 0.70 |

Bold values indicate $p \leq 0.05$.

[a] When soil moisture was controlled for in partial regression analysis, the relationship was no longer significant.

November and June patterns is somewhat counterintuitive as water stress in the dry treatments was higher in summer than in winter. However, collembola generally have long life cycles, and recovery after a disturbance or drought event can take several months (Lindberg and Bengtsson, 2005). We suspect collembola abundance at the time of sampling reflected the integrated response of the community over several months prior to sampling when soil moisture conditions were higher (Fig. 1A).

In contrast to our expectations, we did not find significant effects of warming and elevated [$CO_2$] on abundance of soil microarthropods, and these treatments did not alter the responses to the precipitation treatment. Regression analyses indicated significant relationships between soil microarthropod abundance and soil temperature, thus we were surprised there was not a detectable difference between the warming treatments. There was a large amount of within-treatment variation in microarthropod responses to warming and in the response of soil warming to the treatments; this variation may explain the discrepancy between our statistical tests.

Across treatments, the abundance of collembola was negatively related to soil temperature. This relationship could be explained by temperature-related shifts in soil moisture content. Indeed, while temperature may directly affect survival and reproductive ability of collembola (e.g., van Straalen, 1994), indirect effects through changes in soil moisture may be of higher importance (e.g., Sinclair and Stevens, 2006). For mites, we found a positive relationship between soil temperature and abundance. This relationship was found only in June, and could not be explained by related changes in soil moisture content. We lack data on seasonal mite population dynamics, but it could be that positive effects of increased soil temperature during the preceding winter may have increased mite abundance.

Reported effects of atmospheric [$CO_2$] on soil microarthropods include both negative and positive responses (see reviews: Couteaux and Bolger, 2000; Lindroth, 2010). The concentration of $CO_2$ in the soil is inherently high, thus we did not predict that atmospheric [$CO_2$] would directly impact on the abundance of soil microarthropods (e.g., van Veen et al., 1991). However, in our experiment, elevated [$CO_2$], by regulating soil moisture availability, can reduce the effect of warming and drought on soil moisture content (Dermody et al., 2007). Therefore, positive indirect effects of elevated [$CO_2$] on soil microarthropods through enhanced water availability, and thus, interaction effects of precipitation × [$CO_2$] were expected. Changes in soil moisture in response to [$CO_2$], however were small relative to the precipitation treatment (Dermody et al., 2007), and treatment effects on soil microarthropod abundance via changes in soil moisture were likely minor.

Individual soil microarthropod taxa differed in their responses to our climate change treatments, resulting in altered community composition and richness. Not surprisingly, in November, the highest taxon richness in our study was found in elevated [$CO_2$] and elevated temperature treatments. These treatments had the highest soil moisture content (Fig. 1a; Dermody et al., 2007), and there was a positive correlation between microarthropod richness and soil moisture content. However, the richness patterns in our study must be interpreted with caution. In June, the precipitation treatment had no effect on community richness. Recovery of soil microarthropod communities after severe disturbance predominantly depend on colonization from external species pools (Kardol et al., 2009); however, our experimental design, i.e., open-top chambers, would have constrained recovery through external dispersal. Moreover, in November, abundance and richness of microarthropods were positively related ($R = 0.57$); hence, we cannot exclude the possibility that low community richness in dry treatments was a result of under sampling.

Indirect effects of climate changes on soil microarthropods via changes in plant productivity and community composition might play an important role in net microarthropod responses to climate changes (e.g., Jones et al., 1998; Loranger et al., 2004). In our experiment, aboveground biomass production was generally higher in wet than in dry treatments, and was enhanced by elevated [$CO_2$] and elevated temperature (Kardol et al., 2010a). Moreover, individual plant species differed in their responses resulting in cover dominance shifts (Engel et al., 2009; Kardol et al., 2010b). For example, the cover of *L. cuneata* was much higher in wet than in dry treatments (November: 53% versus 18%; June 51% versus 14%). Previous work in this system showed how shifts in proportional cover of the dominant plant species, in response to the climate change treatments, interacted with direct effects of climate change to shift soil enzyme profiles as well as the taxonomic and functional composition of soil nematode communities (Kardol et al., 2010b). It is likely that changes in plant community composition contributed to the net climate change effects on soil microarthropods by altering both the quality and quantity of resources that plants take up from and return to the soil and by altering abiotic and structural soil conditions (e.g., Hasegawa, 2001; Lindberg et al., 2002; Wardle et al., 2006).

Soil biological responses to climate changes are complex, and have seldom been considered in a realistic, multifactor framework. In this light, our results provide new insights into how simultaneously acting climate change factors may affect an ecologically important group of soil organisms, microarthropods. Most importantly, after long-term applications of our treatments (which allowed for multiple generation of the microarthropods studied), we found that changes in soil moisture, either as direct effect of changes in precipitation regime or as an indirect effect of warming or elevated [$CO_2$], had the largest effect on soil microarthropods, and soil moisture appears to be more important for microarthropod dynamics than the direct effects of warming and elevated [$CO_2$]. However, the observed changes were often subtle, and we emphasize that generalizations about the effects of climate changes on soil microarthropods must be made with caution. Published studies provide conflicting data on soil microarthropod responses to climate changes, with the possibility that responses are specific to particular plant species, communities, or ecosystems. This strongly accentuates the need of more explicit consideration of the environmental and biological context in studies of climate change on soil microarthropods.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.apsoil.2010.11.001.

## References

Badejo, M.A., Akinwole, P.O., 2006. Microenvironmental preferences of oribatid mite species on the floor of a tropical rainforest. Exp. Appl. Acarol. 40, 145–156.

Balogh, J., Balogh, P., 1992. The Oribatid Mites Genera of the World. The Hungarian Natural Museum Press, Budapest.

Bardgett, R.D., Freeman, C., Ostle, N.J., 2008. Microbial contributions to climate change through carbon cycle feedbacks. ISME J. 2, 805–814.

Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W.X., Coleman, D.C., Crossley, D.A., 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecol. Monogr. 62, 569–591.

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

Castro, H.F., Classen, A.T., Austin, E.E., Norby, R.J., Schadt, C.W., 2010. Soil microbial community responses to multiple experimental climate change drivers. Appl. Environ. Microb. 76, 999–1007.

Chikoski, J.M., Ferguson, S.H., Meyer, L., 2006. Effects of water addition on soil arthropods and soil characteristics in a precipitation-limited environment. Acta Oecol. Int. J. Ecol. 30, 203–211.

Christiansen, K., Bellinger, P., 1980–1981. The Collembola of North America North of the Rio Grande, Grinnell College, Iowa.

Classen, A.T., DeMarco, J., Hart, S.C., Whitham, T.G., Cobb, N.S., Koch, G.W., 2006. Impacts of herbivorous insects on decomposer communities during the early stages of primary succession in a semi-arid woodland. Soil Biol. Biochem. 38, 972–982.

Cole, L., Dromph, K.M., Boaglio, V., Bardgett, R.D., 2004. Effect of density and species richness of soil mesofauna on nutrient mineralisation and plant growth. Biol. Fertil. Soils 39, 337–343.

Cotrufo, M.E., Ineson, P., 1995. Effects of enhanced atmospheric $CO_2$ and nutrient supply on the quality and subsequent decomposition of fine roots of *Betula* pendula Roth and Picea sitchensis (Bong). Carr. Plant Soil 170, 267–277.

Coulson, S.J., Hodkinson, I.D., Webb, N.R., Block, W., Bale, J.S., Strathdee, A.T., Worland, M.R., Wooley, C., 1996. Effects of experimental temperature elevation on high-arctic soil microarthropod populations. Polar Biol. 16, 147–153.

Couteaux, M.M., Bolger, T., 2000. Interactions between atmospheric $CO_2$ enrichment and soil fauna. Plant Soil 224, 123–134.

Crossley, D.A., Blair, J.M., 1991. A high-efficiency, low-technology Tullgren-type extractor for soil microarthropods. Agric. Ecosyst. Environ. 34, 187–192.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Dermody, O., Weltzin, J.F., Engel, E.C., Allen, P., Norby, R.J., 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.

Edwards, N.T., Norby, R.J., 1999. Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric $CO_2$ enrichment and elevated air temperature. Plant Soil 206, 85–97.

Engel, E.C., Weltzin, J.F., Norby, R.J., Classen, A.T., 2009. Responses of an old-field plant community to interacting factors of elevated $CO_2$, warming, and soil moisture. J. Plant Ecol. 2, 1–11.

Filser, J., 2002. The role of Collembola in carbon and nitrogen cycling in soil. Pedobiology 46, 234–245.

Frampton, G.K., van den Brink, P.J., Gould, P.J.L., 2000. Effects of spring precipitation on a temperate arable collembolan community analysed using principal response curves. Appl. Soil Ecol. 14, 231–248.

Garten, C.T., Classen, A.T., Norby, R.J., 2009. Soil moisture surpasses elevated $CO_2$ and temperature as a control on soil carbon dynamics in a multi-factor climate change experiment. Plant Soil 319, 85–94.

Garten, C.T., Classen, A.T., Norby, R.J., Brice, D.J., Weltzin, J.F., Souza, L., 2008. Role of $N_2$-fixation in constructed old-field communities under different regimes of [$CO_2$], temperature, and water availability. Ecosystems 11, 125–137.

Hågvar, S., Klanderud, K., 2009. Effect of simulated environmental change on alpine soil arthropods. Global Change Biol. 15, 2972–2980.

Hansen, R.A., Williams, R.S., Degenhardt, D.C., Lincoln, D.E., 2001. Non-litter effects of elevated $CO_2$ on forest floor microarthropod abundances. Plant Soil 236, 139–144.

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

Hasegawa, M., 2001. The relationship between the organic matter composition of a forest floor and the structure of a soil arthropod community. Eur. J. Soil Biol. 37, 281–284.

Huhta, V., Hänninen, S.M., 2001. Effects of temperature and moisture fluctuations on an experimental soil microarthropod community. Pedobiology 45, 279–286.

IPCC [Intergovernmental Panel on Climate Change], 2007. Climate Change 2007: The Physical Science Basis. Cambridge University Press, Cambridge, UK.

Jones, T.H., Thompson, L.J., Lawton, J.H., Bezemer, T.M., Bardgett, R.D., Blackburn, T.M., Bruce, K.D., Cannon, P.F., Hall, G.S., Hartley, S.E., Howson, G., Jones, C.G., Kampichler, C., Kandeler, E., Ritchie, D.A., 1998. Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. Science 280, 441–443.

Kardol, P., Newton, J.S., Bezemer, T.M., van der Putten, W.H., 2009. Contrasting diversity patterns of soil mites and nematodes in secondary succession. Acta Oecol. 35, 603–609.

Kardol, P., Campany, C.E., Souza, L., Norby, R., Weltzin, J.F., Classen, A.T., 2010a. Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental oldfield ecosystem. Global Change Biol. 16, 2676–2687.

Kardol, P., Cregger, M.A., Campany, C.E., Classen, A.T., 2010b. Soil ecosystem functioning under climate change: plant species and community effects. Ecology 91, 767–781.

Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, United Kingdom.

Lindberg, N., Bengtsson, J., 2005. Population responses of oribatid mites and collembolans after drought. Appl. Soil Ecol. 28, 163–174.

Lindberg, N., Bengtsson, J., 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.

Lindroth, R.L., 2010. Impacts of elevated atmospheric $CO_2$ and $O_3$ on forests: phytochemistry, trophic interactions, and ecosystem dynamics. J. Chem. Ecol. 36, 2–21.

Loranger, G.I., Pregitzer, K.S., King, J.S., 2004. Elevated $CO_2$ and $O_{3t}$ concentrations differentially affect selected groups of the fauna in temperate forest soils. Soil Biol. Biochem. 36, 1521–1524.

Lussenhop, J., Treonis, A., Curtis, P.S., Teeri, J.A., Vogel, C.S., 1998. Response of soil biota to elevated atmospheric $CO_2$ in poplar model systems. Oecologia 113, 247–251.

Moron-Rios, A., Rodriguez, M.A., Perez-Camacho, L., Rebollo, S., 2010. Effects of seasonal grazing and precipitation regime on the soil macroinvertebrates of a Mediterranean old-field. Eur. J. Soil Biol. 46, 91–96.

Niedbala, W., 2002. Ptyctimous Mites (Acari, Oribatida) of the Nearctic Region. Monographs of the Upper Silisian Museam, No. 4, Bytom.

Norby, R.J., Edwards, N.T., Riggs, J.S., Abner, C.H., Wullschleger, S.D., Gunderson, C.A., 1997. Temperature-controlled open-top chambers for global change research. Global Change Biol. 3, 259–267.

O'Lear, H.A., Blair, J.M., 1999. Responses of soil microarthropods to changes in soil water availability in tallgrass prairie. Biol. Fertil. Soils 29, 207–217.

Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39, 287–388.

Pflug, A., Wolters, V., 2001. Influence of drought and litter age on Collembola communities. Eur. J. Soil Biol. 37, 305–308.

Sackett, T.E., Classen, A.T., Sanders, N.J., 2010. Linking soil food web structure to above- and below-ground ecosystem processes: a meta-analysis. Oikos, doi:10.1111/j.1600-0706.2010.18728.x.

Schröter, D., Brussaard, L., De Deyn, G., Poveda, K., Brown, V.K., Berg, M.P., Wardle, D.A., Moore, J., Wall, D.H., 2004. Trophic interactions in a changing world: modeling aboveground–belowground interactions. Basic Appl. Ecol. 5, 515–528.

Seastedt, T.R., 1984. The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. 29, 25–46.

Sinclair, B.J., Stevens, M.I., 2006. Terrestrial microarthropods of Victoria Land and Queen Maud Mountains Antarctica: implications of climate change. Soil Biol. Biochem. 38, 3158–3170.

Sjursen, H., Michelsen, A., Jonasson, S., 2005. Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. Appl. Soil Ecol. 30, 148–161.

ter Braak, C., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca, NY, USA.

Tsiafouli, M.A., Kallimanis, A.S., Katana, E., Stamou, G.P., Sgardelis, S.P., 2005. Responses of soil microarthropods to experimental short-term manipulations of soil moisture. Appl. Soil Ecol. 29, 17–26.

Uvarov, A.V., 2003. Effects of diurnal temperature fluctuations on population responses of forest floor mites. Pedobiology 47, 331–339.

van Straalen, N.M., 1994. Adaptive significance of temperature responses in Collembola. Acta Zool. Fennica 195, 135–142.

van Veen, J.A., Liljeroth, E., Lekkerkerk, L.J.A., Van de Geijn, S.C., 1991. Carbon fluxes in plant-soil systems at elevated atmospheric $CO_2$ levels. Ecol. Appl. 1, 175–181.

Wan, S., Norby, R.J., Ledford, J., Weltzin, J.F., 2007. Responses of soil respiration to elevated $CO_2$, air warming, and changing soil water availability in a model old-field grassland. Global Change Biol. 13, 2411–2424.

Walter, D.E., Proctor, H.C., 1999. Mites. Ecology, Evolution and Behaviour. CABI Publishing, Wallingford, Oxon, UK.

Wardle, D.A., Yeates, G.W., Barker, G.M., Bonner, K.I., 2006. The influence of plant litter diversity on decomposer abundance and diversity. Soil Biol. Biochem. 38, 1052–1062.