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Soil ecosystem functioning under climate change: plant species and community effects

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Abstract. Feedbacks of terrestrial ecosystems to atmospheric and climate change depend on soil ecosystem dynamics. Soil ecosystems can directly and indirectly respond to climate change. For example, warming directly alters microbial communities by increasing their activity. Climate change may also alter plant community composition, thus indirectly altering the soil communities that depend on their inputs. To better understand how climate change may directly and indirectly alter soil ecosystem functioning, we investigated old-field plant community and soil ecosystem responses to single and combined effects of elevated [CO_2], warming, and precipitation in Tennessee (USA). Specifically, we collected soils at the plot level (plant community soils) and beneath dominant plant species (plant-specific soils). We used microbial enzyme activities and soil nematodes as indicators for soil ecosystem functioning.

Our study resulted in two main findings: (1) Overall, while there were some interactions, water, relative to increases in [CO_2] and warming, had the largest impact on plant community composition, soil enzyme activity, and soil nematodes. Multiple climate-change factors can interact to shape ecosystems, but in our study, those interactions were largely driven by changes in water. (2) Indirect effects of climate change, via changes in plant communities, had a significant impact on soil ecosystem functioning, and this impact was not obvious when looking at plant community soils. Climate-change effects on enzyme activities and soil nematode abundance and community structure strongly differed between plant community soils and plant-specific soils, but also within plant-specific soils.

These results indicate that accurate assessments of climate-change impacts on soil ecosystem functioning require incorporating the concurrent changes in plant function and plant community composition. Climate-change-induced shifts in plant community composition will likely modify or counteract the direct impact of atmospheric and climate change on soil ecosystem functioning, and hence, these indirect effects should be taken into account when predicting the manner in which global change will alter ecosystem functioning.

Key words: elevated [CO_2]; extracellular enzymes; Festuca pratense; *global warming;* Lespedeza cuneata; *multifactor experiment; nematodes; Oak Ridge, Tennessee, USA; old fields; open-top chambers; precipitation; redundancy analysis.*

Introduction

The climate is changing due to anthropogenic impacts: rising levels of atmospheric [CO_2] are leading to increasing global temperatures and changes in the hydrologic cycle (IPCC 2007). Long-term ecosystem responses and subsequent feedbacks to atmospheric and climate changes (hereafter referred to as "climate changes") may depend on how the soil system responds to these perturbations, i.e., increase in belowground carbon (C) input may decrease feedbacks to the global C cycle, whereas increases in decomposition and mineralization of organic matter may increase feedbacks to the C cycle (Davidson and Janssens 2006, Bardgett et al. 2008, De Deyn et al. 2008).

Soil processes, such as decomposition and nutrient cycling, are, at the local level, driven by soil organisms, their interactions with plants (dead or alive), and abiotic soil conditions such as temperature and moisture (Wardle 2002). Climate changes may directly, by changes in soil abiotic conditions, or indirectly, by changes in plant community composition, alter soil processes and the organisms that mediate these processes. Previous work shows that changes in climate may alter soil processes and the soil organisms that drive these processes (e.g., Schimel et al. 1994, Jones et al. 1998); however, these studies have focused on simple (often single-species) ecosystems (e.g., Austin et al. 2009) or on samples collected to integrate the response of the entire plant community (Henry et al. 2005, Niklaus et al. 2007, Ayres et al. 2008). While these studies are useful in exploring potential mechanisms (single-species experiments) or net effects (integrated response), they exclude

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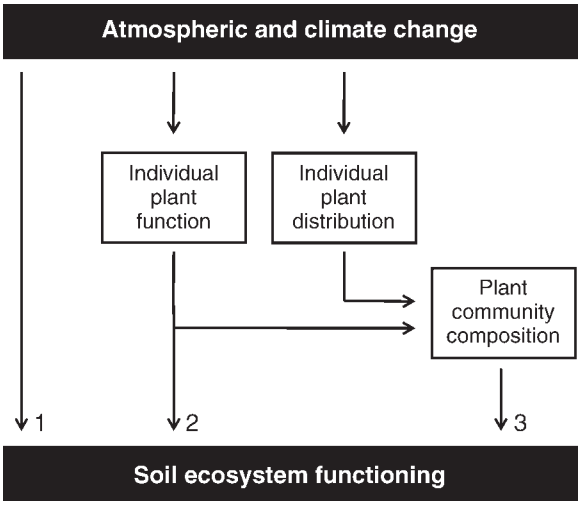

FIG. 1. Conceptual diagram. Atmospheric and climate change can impact soil ecosystem functioning by directly affecting biological activity and composition of soil communities, (pathway 1) or by affecting individual plant functioning (e.g., root biomass production) (pathway 2). Atmospheric and climate change can also impact soil ecosystem functioning through shifts in plant community composition (pathway 3), which can result from changes in individual plant function (altered plant-competitive interactions) or from changes in individual plant distribution (species range shifts). Changes in individual plant distribution are not a focus of this paper.

the manner in which individual plant responses to climate change may alter soil ecosystem functioning (Johnson et al. 2008, Antoninka et al. 2009).

In this paper, we simultaneously consider multiple pathways involved in climate-change effects on soil ecosystem functioning (Fig. 1). Climate changes can directly influence the functioning of soil organisms, their competitive interactions, and community composition by changing the abiotic conditions of the soil environment (Fig. 1, pathway 1). Climate changes can also influence individual plant function, which then can indirectly influence soil ecosystem functioning (Fig. 1, pathway 2). For example, altered plant physiology or phenology can change the quality or quantity of resources plants deliver to or take up from the soil (Cotrufo and Ineson 1995). Moreover, variation among plant species in their physiological or phenological responses to climate change (e.g., Hunt et al. 1991) can alter plant competitive interactions, and hence, plant community composition (e.g., Dukes and Hungate 2002, Morecroft et al. 2004, Walker et al. 2006, Williams et al. 2007). Additional changes in plant community composition in response to climate change can result from effects on individual plant distribution, such as poleward or elevational shifts in response to warming (Parmesan and Yohe 2003, Hickling et al. 2006). Since individual plant species differ in their effects on soil abiotic and biotic properties (e.g., Drigo et al. 2007, Kardol et al. 2007, Johnson et al. 2008), changes in plant community composition in response to climate changes can have strong effects on the functioning of soil ecosystems (Fig. 1, pathway 3).

Interactions among multiple climate-change factors, such as changes in [CO_2], temperature, and precipitation regimes, can affect plants and soils in ways that are not easily predictable from measuring a single factor (e.g., Pendall et al. 2004, Fenner et al. 2007). Such interactive effects may impair the predictability of climate-change impacts on soil ecosystem functioning. For example, increased soil temperature predicts enhanced decomposition and mineralization via increased microbial activity (e.g., Fierer et al. 2005); however, these changes depend upon soil water availability. Hence, effects of warming on soil ecosystem processes are less predictable when increased evapotranspiration results in soil drying. Similarly, enhanced plant productivity under elevated [CO_2] through increased photosynthetic efficiency (Field et al. 1995) could be moderated if concurrent changes in precipitation regimes result in plant water stress (De Boeck et al. 2008). Because climate change will include multiple simultaneous changes in [CO_2], temperature, and precipitation regimes, multifactor experiments are needed to better understand climate-change impacts on soil ecosystem functioning (Dermody 2006).

We took advantage of a long-term, multifactor climate-change experiment in a constructed old-field ecosystem to test the hypothesis that direct and plant-mediated effects of climate changes on soil ecosystem functioning (Fig. 1, pathways 1 and 2) interact with or depend upon concurrent shifts in plant community composition (Fig. 1, pathway 3). We manipulated CO_2 concentrations (ambient, elevated), temperature (ambient, elevated), and precipitation (wet, dry) in open-top chambers planted with a diverse old-field community. First we measured the response of plant species cover to understand how the treatments alter plant community composition. Second, as an indicator for soil function (e.g., soil nutrient cycling), we measured the enzyme activity of soil microbial communities in soils collected at the plot level (to test the integrated soil response; hereafter "plant community soils") and in soils collected directly beneath dominant plant species (to test the plant-specific soil response; hereafter "plant-specific soils"). Plant community soils represent net climate-change effects (i.e., all three pathways presented in Fig. 1), while plant-specific soils represent direct effects and effects via change in individual plant function (pathways 1 and 2 in Fig. 1). As an indicator for soil food web structure and function, we analyzed soil nematode communities. We compared the responses of the indicators for soil function both between plant community soils and plant-specific soils and between plant-specific soils from different origin.

METHODS

Experimental setup

The Old-Field Community, Climate, and Atmosphere Manipulation Experiment was established at the Oak

Ridge National Environmental Research Park (35°54′12″ N, 84°20′22″ W) in Oak Ridge, Tennessee, USA. The site was abandoned from agricultural use in 1943 and left fallow until 1964 when a managed fescue field was established. The soil is classified as Captina silt loam with moderate-to-medium granular structure and medium internal drainage. Whole soil N (1.62 g N/kg), C (18.3 g C/kg), and C:N ratio (11.4), 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. 2008, 2009). Precipitation is generally evenly distributed throughout the year, with an annual mean of 1322 mm; the mean July maximum temperature is 31.2°C, and the mean January minimum temperature is −2.7°C.

Twelve experimental plots were established in 2002. Trenches were cut 75 cm deep around each 4 m diameter plot and through the center, thereby defining two 6.3 m^2 experimental units (split plots). The existing vegetation at the site was killed using glyphosate, and dead biomass was extracted to remove meristems and some of the seed bank. Plots were planted with seven plant species: *Plantago lanceolata* L., a herbaceous forb; *Andropogon virginicus* L., a 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* L., a herbaceous forb; and *Lespedeza cuneata* (Dum. Cours.) G. Don, a N_2-fixing subshrub (hereafter referred to by genus names). These plant species were chosen because (1) they are common eastern old-field species and are common at our field site (cf. Jongen and Jones 1998; L. Souza, *unpublished data*); (2) they or their congeners are common worldwide; (3) they or their congeners have been the focus of previous climate-change research (Poorter and Perez-Soba 2001); and (4) they comprise a variety of "functional types." Native plant status was not a criterion in selecting the species; we selected species that were common species to our area and representative of old fields. Greenhouse-grown seedlings of all seven species were transplanted into the plots in August 2002 and April 2003 in a predetermined grid such that seedlings were 18 cm apart with no adjacent conspecifics (Engel et al. 2009). Approximately 170 individuals were planted per plot. In autumn 2005, 2006, and 2007, aboveground plants were harvested by clipping the shoot 5 cm above the soil surface to mimic grazing.

In May 2003, [CO_2], temperature, and soil moisture treatments were applied through the use of open-top chambers (OTCs), which were installed on each plot. The OTCs were constructed of aluminum frames (4 m in diameter, 2.2 m in height) covered with clear PVC panels; the double-walled panel on the lower half of each OTC was perforated on the inner wall with holes through which air of the appropriate temperature and CO_2 concentration was blown into the chambers. Whole plots received treatments of ambient or elevated [CO_2] (ambient + 300 ppm) in combination with ambient or elevated temperature (ambient + 3°C) in a randomized, complete-block design ($n = 3$). An open-sided shelter was assembled over each OTC to exclude precipitation. Each split plot within each whole plot was randomly assigned to one of two soil moisture treatments (wet or dry) created by differential irrigation, i.e., 2 mm or 25 mm per week. Air and soil temperature, [CO_2], and soil volumetric water content were continuously monitored. Additional information on the experimental design can be found in Wan et al. (2007).

Between 1 April and 30 October 2007, the focal period of this study, daytime [CO_2] averaged 419 ppm in ambient [CO_2] chambers and 757 ppm in elevated [CO_2] chambers. For the same period, air temperature averaged 20.7°C in chambers with ambient temperature and 23.8°C in chambers with elevated temperature; soil temperature (at 10 cm depth) averaged 20.5°C and 22.6°C, respectively. Soil volumetric water content (0–10 cm depth) averaged 11.6% in dry treatments and 16.4% in wet treatments.

Plant community composition

As a proxy for plant community composition four years after the treatments were initiated, we visually estimated percentage cover for each of the seven plant species based on a modified Domin-Krajina cover scale (Engel et al. 2009). Cover data were recorded monthly during the 2007 growing season (April to October).

Soil sampling

In October 2007, to measure integrated soil responses to the climate-change treatments, three soil cores (2 cm in diameter, 10 cm in depth) were collected in each treatment and bulked: "plant community soils." In each treatment, one core was collected in the front, one in the middle, and one in the back of the plot. Within each location, samples were randomly located regarding the spatial configuration of the plant species. Samples were generally located in spaces between individual plants. Therefore, the bulked samples included soils from the influence zone of multiple plant species. To measure plant-specific soil responses, three additional cores were collected and bulked from under each of the two dominant plant species, *Lespedeza* and *Festuca*, from the center of randomly located monoculture patches: "plant-specific soils." For logistic reasons, plant community soils were collected one week before plant-specific soils. After collection, soil samples were stored on ice and returned to the laboratory. After homogenizing within individual samples, a subsample was collected for nematode analyses. Remaining soils were sieved (2 mm) and stored at 4°C for ~15 h prior to measuring extracellular enzyme activities. From the sieved soils, a 15-g subsample was oven-dried for 48 h to determine soil gravimetric water content.

Soil ecosystem functioning: extracellular enzyme activities

To determine how treatments alter microbial activity, we measured potential activity of the following ecologically relevant extracellular enzymes using methods described by Saiya-Cork et al. (2002): β-glucosidase, cellobiohydrolase, β-xylosidase, α-glucosidase, phosphatase, N-acetylglucosaminidase (NAGase), sulfatase, peroxidase, and phenol oxidase. The first seven enzymes were measured using methylumbelliferone-linked substrates. Activity of peroxidase and phenol oxidase was measured using L-3,4-dihydroxyphenylalanine. β-Glucosidase, cellobiohydrolase, β-xylosidase, α-glucosidase assist with the breakdown of energy sources such as carbohydrates and polysaccharides, making them more readily available for uptake by soil organisms. NAGase is a chitinolytic enzyme involved in the mineralization of N from chitin. Phosphatase is involved in the release of inorganic P. Sulfatase is involved in the release of inorganic forms of sulfur. Peroxidase and phenol oxidase assist in the decomposition of lignin. Enzyme activities were assayed fluorimetrically, except for peroxidase and phenol oxidase, which were assayed spectrophotometrically. Briefly, field-moist soil (1 g) was suspended in 125 mL of 0.05 mol/L sodium acetate buffer (pH 5). Soil suspension (200 μL) was added to microplates that contained solutions necessary for a blank, a negative control, and a quenching standard. Microplates were incubated in total darkness at room temperature. Duration of incubation depended upon the optimal temperature for each enzyme: 30 min for NAGase and phosphatase, 2 h for β-glucosidase, cellobiohydrolase, β-xylosidase, α-glucosidase, and sulfatase, and 24 h for peroxidase and phenol oxidase.

Soil ecosystem functioning: nematodes

To determine the manner in which our treatments affect soil organisms at higher trophic levels and as indicator for soil food web functioning, we extracted nematodes. Nematodes were extracted from ~150 g of soil using a sugar flotation method, heat-killed, and fixed using 35% formaldehyde diluted to 4%. At least 150 randomly selected individuals in each sample were identified to family or genus level and allocated to feeding group according to Yeates et al. (1993): endo-parasitic plant feeders, ecto-parasitic plant feeders, root hair feeders ("plant-associated nematodes"), bacterial feeders, fungal feeders, and omni-carnivores. We expressed their numbers per 100 g dry soil.

Data analysis

The direct and interactive effects of $[CO_2]$, temperature, and water on percent cover of *Lespedeza* and *Festuca* were tested using a three-way repeated-measures, split-plot analysis of variance (ANOVA) (PROC MIXED, SAS Institute, Cary, North Carolina, USA). Percent cover data were arcsine-transformed to meet assumptions of normality and homogeneity of variance.

Plant community soils and plant-specific soils were analyzed separately. All data collected in the plant community soils were analyzed using a three-way, split-plot ANOVA (PROC MIXED). Data collected in plant-specific soils were tested using a four-way, split-plot ANOVA (PROC MIXED). ANOVA analyses were run with a combined random-effects and fixed-effects model including the Kenward-Rogers adjustment for degrees of freedom. For phosphatase, cellobiohydrolase, α-glucosidase, phenol oxidase, endo-parasitic plant feeders, and fungal feeders (plant community soils), and for phosphatase, α-glucosidase, total number of nematodes, root hair feeders, and bacterial feeders (plant-specific soils), data were log-transformed to meet assumptions of normality and homogeneity of variance.

Treatment effects on plant community composition were analyzed as repeated measures in redundancy analyses (RDA), including treatments and their interactions as interactive terms with time as explanatory variables. For plant-specific soils, treatment and plant species (*Lespedeza*, *Festuca*) effects on composition of enzyme activities, nematode feeding groups, and nematode taxa were analyzed using RDA, including treatments, plant species, and their interactions as explanatory variables. "Species" data (i.e., enzyme activities, nematode numbers) were log-transformed. 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 test, samples were permuted within blocks. Marginal effects (i.e., the independent effect of each variable) were tested by manual selection of each individual variable. For plant community composition, we used permutation tests restricted for split-plot design reflecting our repeated measurements. The RDA analyses were performed using CANOCO, version 4.5 (Ter Braak and Šmilauer 2002).

Results

Plant community composition

After four years, >20% of the variation in plant community composition was explained by the climate-change treatments (Table 1). The analysis of individual terms showed significant interactions between $[CO_2]$ and water and between temperature and water. However, the single effect of water had the highest explanatory power for plant community composition, explaining 12% of the total variation. $[CO_2]$ and temperature did not directly influence plant community composition. Plant community responses to climate-change treatments could be attributed to differential responses of *Lespedeza cuneata* and *Festuca pratense*, which were the most dominant species in the community.

Averaged across the season, *Lespedeza* and *Festuca* together accounted for 63% of total plant cover, followed in dominance by *Trifolium* (16%), *Plantago* (7%), *Andropogon* (6%), *Dactylis* (5%), and *Solidago* (3%). Seasonal patterns of plant species proportional

TABLE 1. Redundancy analyses of treatment effects and their interactions on plant community composition across the 2007 growing season.

Explanatory variable	Expl. var. (%)	*F* ratio	*P*
$[CO_2]$	2.2	3.85	0.44
Temperature (*T*)	3.3	5.00	0.22
H_2O	12.2	20.70	<0.01
$[CO_2] \times T$	3.0	4.56	0.22
$[CO_2] \times H_2O$	7.2	11.50	0.01
$T \times H_2O$	8.4	13.51	<0.01
$[CO_2] \times T \times H_2O$	5.2	8.98	0.06
Full model	22.8	6.04	0.02

Notes: Each factor was tested as an interactive term with time, reflecting the repeated measurements. Marginal effects (i.e., effects when a term is used as the only explanatory variable) and results of the full model including all explanatory variables are presented. Expl. var. (%) is the percentage of variation explained. *P* values are based on Monte Carlo permutation tests. The study was conducted in the Oak Ridge National Environmental Research Park in Oak Ridge, Tennessee, USA.

cover across wet and dry treatments are shown in Appendix A. Because species other than *Lespedeza* and *Festuca* made up a relatively small proportion of the plant community and did not contribute much to the plant community response, they will not be discussed here (see Engel et al. [2009] for community response details). From April to October, proportional cover of *Lespedeza* became higher in wet relative to dry treatments ($H_2O \times$ time, $F_{1,120} = 7.77$, $P < 0.01$; Fig. 2). There was a marginal $[CO_2] \times$ time interaction ($F_{1,120} = 3.11$, $P = 0.08$) where there was higher proportional cover of *Lespedeza* under ambient than under elevated $[CO_2]$ early in the season. Proportional cover of *Festuca* was higher in wet relative to dry treatments early in the season, but this pattern reversed toward the end of the season, leading to a significant time $\times$ H_2O interaction ($F_{1,120} = 9.01$, $P < 0.01$; Fig. 2). Proportional cover of *Festuca* was marginally higher at elevated relative to ambient temperature (*T*) ($F_{1,39.4} = 3.76$, $P = 0.06$), and there was a marginally significant $[CO_2] \times T \times$ time interaction ($F_{1,120} = 3.65$, $P = 0.06$). Other single and interactive effects of climate-change treatments on the proportional cover of *Lespedeza* and *Festuca* were not significant.

Soil ecosystem functioning

Extracellular enzyme activities.—We used extracellular enzyme activities as indicators of soil function. In plant community soils, the activity of one out of nine enzymes was significantly affected by the climate-change treatments (Fig. 3A; Appendices B and C). Activity of β-xylosidase was lower in dry than in wet treatments, but only under elevated $[CO_2]$ ($[CO_2] \times H_2O$, $F_{1,14} = 5.09$, $P = 0.04$) or under elevated temperature ($T \times H_2O$, $F_{1,14} = 7.64$, $P = 0.02$). In treatments with ambient $[CO_2]$, β-xylosidase activity was lower under elevated temperature than under ambient temperature, while in treatments with elevated $[CO_2]$, activity was higher under elevated temperature than under ambient temperature ($[CO_2] \times T$, $F_{1,14} = 5.82$, $P = 0.03$).

Overall, enzyme activities were higher in plant-specific soils than in plant community soils, and the impact of the climate-change treatments was generally stronger in plant-specific soils relative to plant community soils (Fig. 3B; Appendices B and C). In plant-specific soils, activity of phosphatase ($F_{1,24} = 36.37$, $P < 0.01$), sulfatase ($F_{1,24} = 17.71$, $P < 0.01$), phenol oxidase ($F_{1,24} = 9.00$, $P = 0.01$), and peroxidase ($F_{1,30} = 20.36$, $P < 0.01$) was lower in dry than in wet treatments, while activity of cellobiohydrolase was higher in dry than in wet treatments ($F_{1,24} = 5.88$, $P = 0.03$). Similar to plant community soils, we found few effects of $[CO_2]$ and temperature on enzyme activities in plant-specific soils. However, activity of β-glucosidase was higher under

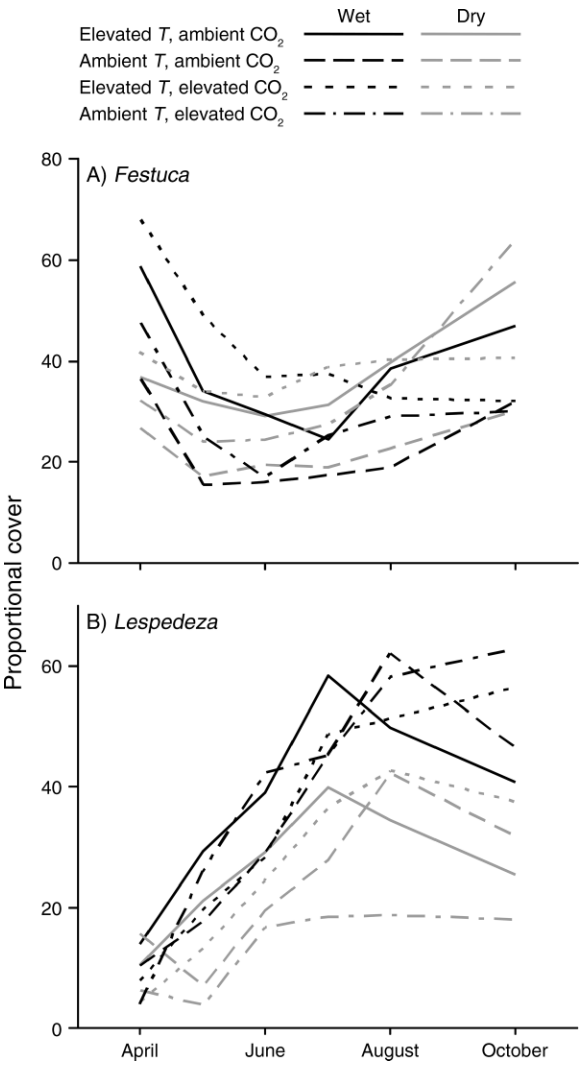

FIG. 2. Proportional cover of (A) *Festuca pratense* and (B) *Lespedeza cuneata* from April to October 2007 for all combinations of $[CO_2]$, temperature (*T*), and H_2O treatments. The study was conducted in the Oak Ridge National Environmental Research Park in Oak Ridge, Tennessee, USA.

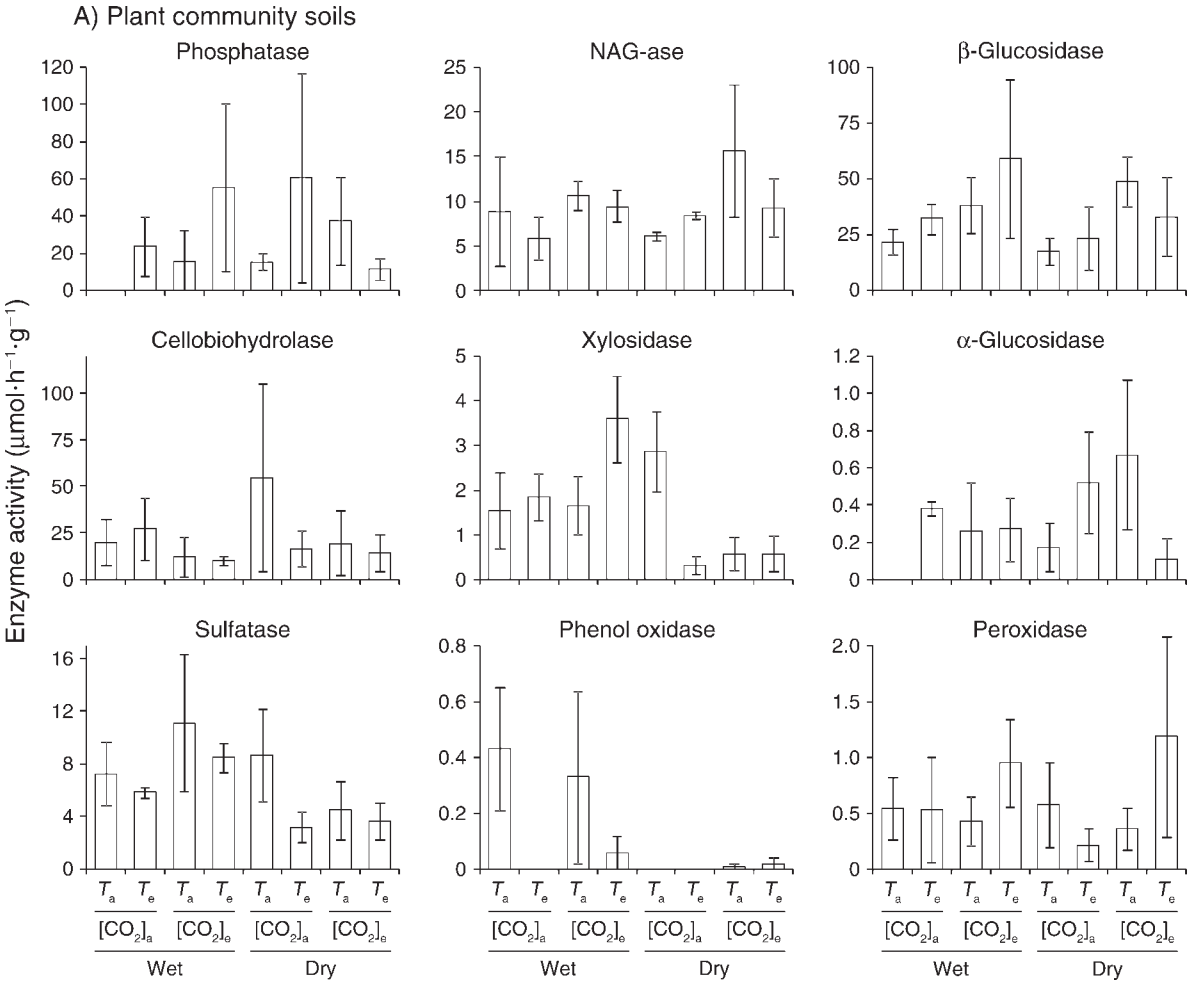

FIG. 3. Enzyme activities in (A) plant community soils and (B) plant-specific soils (i.e., soils beneath *Lespedeza* and beneath *Festuca*) under $[CO_2]$, temperature (T), and H_2O treatments. Data are means ± SE ($n = 3$). Abbreviations are: T_a, ambient temperature; T_e, elevated temperature; $[CO_2]_a$, ambient $[CO_2]$; $[CO_2]_e$, elevated $[CO_2]$; NAG-ase, N-acetylglucosaminidase.

elevated $[CO_2]$ than under ambient $[CO_2]$ ($F_{1,14} = 4.64$, $P = 0.04$). For β-glucosidase, there was a significant $H_2O \times T \times$ species interaction ($F_{1,24} = 7.63$, $P = 0.01$) and for NAGase there was a significant species × $[CO_2] \times T$ interaction ($F_{1,24} = 7.64$, $P = 0.02$). In plant-specific soils, enzyme activity was higher in *Festuca* soils relative to *Lespedeza* soils for four out of nine enzymes (phosphatase, $F_{1,24} = 17.19$, $P < 0.01$; NAGase, $F_{1,24} = 11.01$, $P = 0.01$; β-glucosidase, $F_{1,24} = 24.20$, $P < 0.01$; sulfatase, $F_{1,24} = 5.85$, $P = 0.03$; Fig. 3B; Appendices B and C).

In plant-specific soils, when enzyme activities were analyzed for composition, the full RDA model, including $[CO_2]$, temperature, water, and plant species as explanatory factors, explained >40% of the variation. Both water and plant species explained a significant amount of the variation, and there was a significant H_2O × species interaction (Table 2). Similarly, we found significant $[CO_2]$ × species and $[CO_2] \times H_2O \times$ species interactions. These species × treatment interactions indicate plant-specific profiles of enzyme activities in response to the climate-change treatments (Fig. 4). Phosphatase, cellobiohydrolase, and β-glucosidase contributed most to the overall enzyme profile response. At the community level, there was also a significant interactive effect of $[CO_2]$ and water (Table 2).

The complete ANOVA results for enzyme activities are given in Appendix C.

Nematodes.—We used nematode abundance and community composition as indicators for soil food web structure and function. In plant community soils, we found several significant interactions among the climate-change treatments on nematode numbers (Fig. 5A; Appendices D and E). However, water had the strongest effect overall. The total number of nematodes was lower in dry than in wet treatments, except for treatments with elevated $[CO_2]$ and ambient temperature ($[CO_2] \times T \times H_2O$, $F_{1,16} = 7.27$, $P = 0.02$). Treatment effects differed considerably across feeding groups. Under ambient $[CO_2]$, numbers of endoparasites were lower in dry than in wet treatments ($[CO_2] \times H_2O$, $F_{1,8} =$

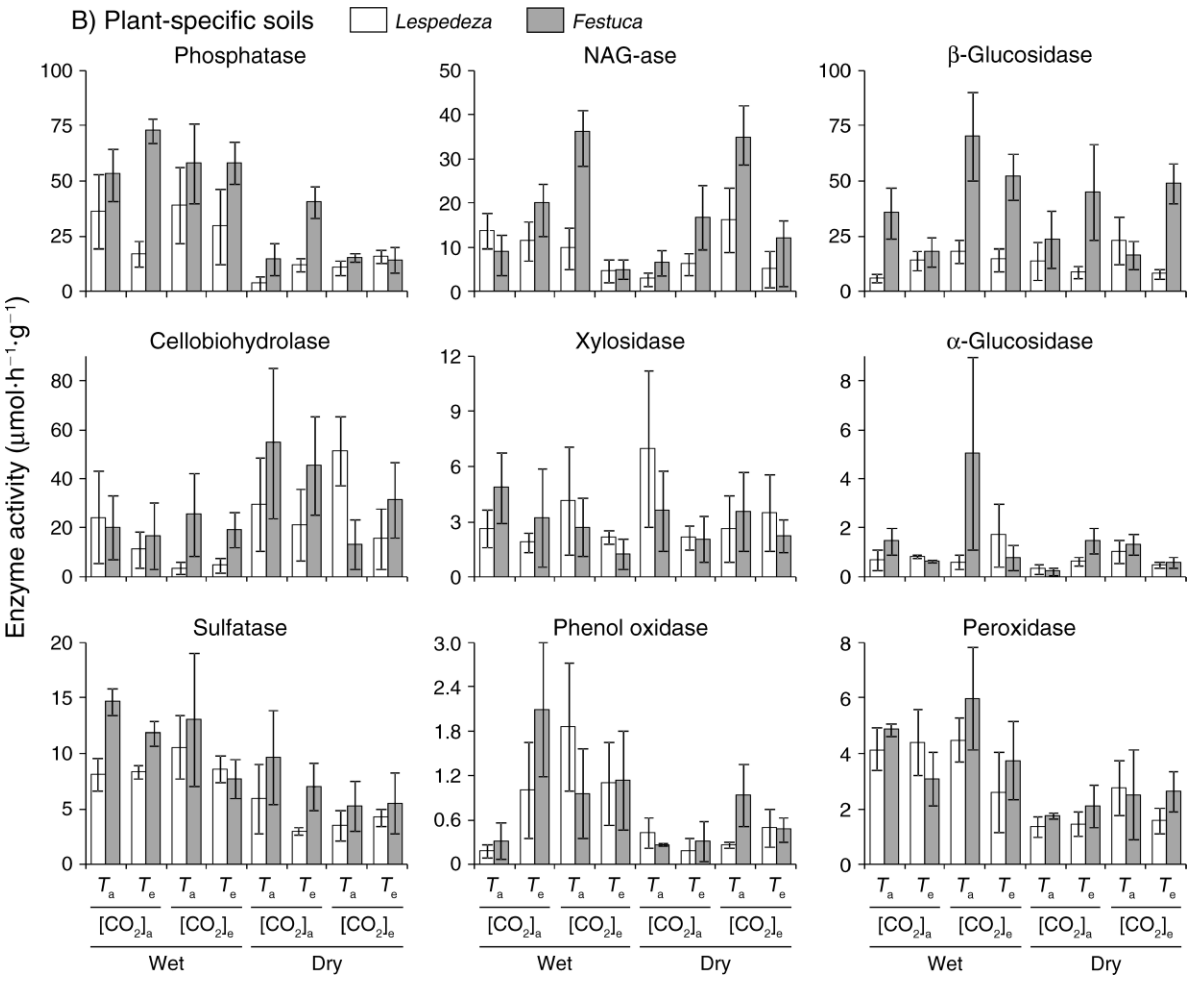

FIG. 3. Continued.

TABLE 2. Results from redundancy analyses of climate-change treatments and plant species impacts (Species; i.e., *Lespedeza* or *Festuca*) and their interactions on enzyme activities, nematode feeding groups, and nematode taxa.

	Enzyme activities			Nematode feeding groups			Nematode taxa		
Explanatory variable	Expl. var. (%)	*F* ratio	*P*	Expl. var. (%)	*F* ratio	*P*	Expl. var. (%)	*F* ratio	*P*
$[CO_2]$	1.7	0.79	0.55	1.5	0.57	0.57	1.8	0.83	0.62
Temperature (*T*)	1.7	0.81	0.54	2.5	1.25	0.27	3.2	1.52	0.11
H_2O	11.5	5.96	<0.01	27.1	18.19	<0.01	15.9	8.87	<0.01
Species	7.8	3.85	<0.01	5.9	3.01	0.02	3.9	1.90	0.06
$[CO_2] \times T$	2.6	1.24	0.27	0.5	0.23	0.96	1.7	0.78	0.64
$[CO_2] \times H_2O$	5.6	2.69	0.02	12.9	7.15	<0.01	6.7	3.33	<0.01
$[CO_2] \times$ species	4.9	2.35	0.04	1.8	0.87	0.46	1.4	0.66	0.79
$T \times H_2O$	3.4	1.61	0.15	4.6	2.32	0.07	5.1	2.50	0.01
$T \times$ species	4.4	2.10	0.06	4.0	1.98	0.09	3.5	1.67	0.08
$H_2O \times$ species	10.2	5.23	<0.01	17.3	10.12	<0.01	9.6	4.97	<0.01
$[CO_2] \times T \times H_2O$	2.2	1.05	0.41	2.7	1.32	0.23	2.4	1.14	0.28
$[CO_2] \times T \times$ species	3.7	1.78	0.11	0.7	0.35	0.89	1.6	0.77	0.66
$[CO_2] \times H_2O \times$ species	6.3	3.10	<0.01	9.3	4.92	<0.01	4.5	2.19	0.02
$T \times H_2O \times$ species	4.2	2.02	0.07	3.2	1.59	0.16	3.9	1.91	0.06
$[CO_2] \times T \times H_2O \times$ species	2.9	1.37	0.23	2.0	0.99	0.40	2.2	1.02	0.37
Full model	40.5	1.44	0.02	55.3	2.93	<0.01	46.8	1.93	<0.01

Notes: Marginal effects (effects when a term is used as the only explanatory variable) and results of the full models including all explanatory variables are presented. Expl. var. (%) is the percentage of variation explained. *P* values are based on Monte Carlo permutation tests.

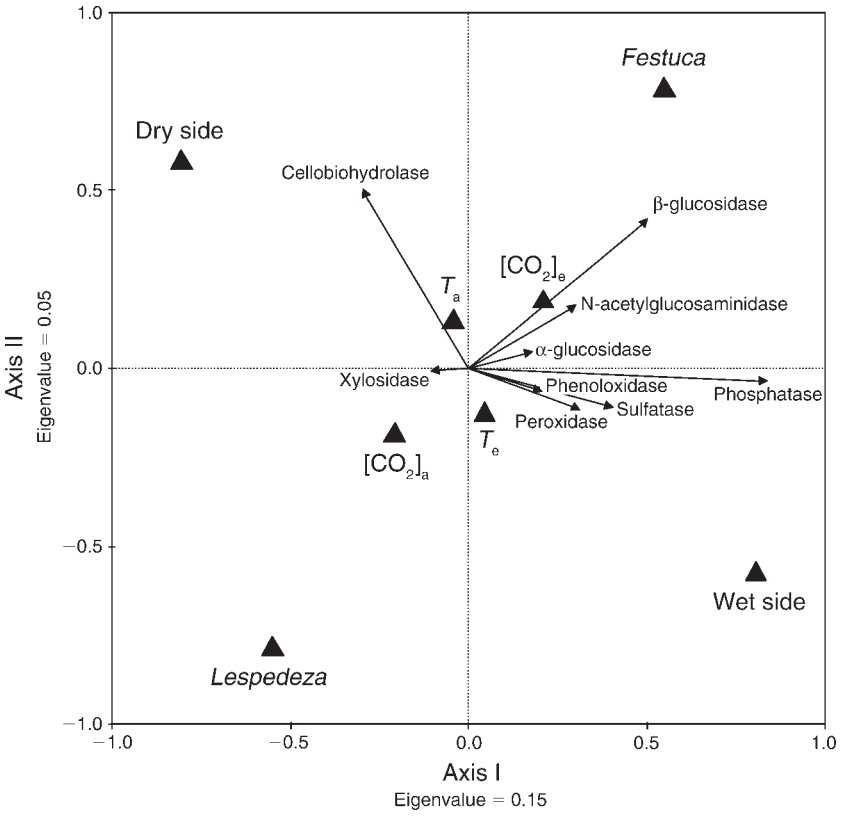

FIG. 4. Species–treatment plot resulting from the redundancy analysis of soil enzyme activities. Treatments included are $[CO_2]$, temperature (T), H_2O, and plant species (*Lespedeza* and *Festuca*). For clarity, treatment interactions are not shown. Eigenvalues along the axes indicate the amount of explained variability in enzyme activities. Triangles represent the centroid position of the climate-change treatments and the plant species.

6.66, $P = 0.03$) and lower under elevated than under ambient temperature ($[CO_2] \times T$, $F_{1,8} = 8.22$, $P < 0.01$); there were no effects of water and temperature under elevated $[CO_2]$. Under elevated T, numbers of root hair-feeders were lower in dry than in wet treatments ($T \times H_2O$, $F_{1,16} = 11.74$, $P < 0.01$) and lower under ambient than under elevated $[CO_2]$ ($[CO_2] \times T$, $F_{1,16} = 4.62$, $P = 0.05$); there were no effects of water and $[CO_2]$ under ambient temperature. For bacterial feeders, there were several significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) effects of the climate-change treatments, which strongly reflected the pattern of the total number of nematodes: lower numbers in dry than in wet treatments, except for treatments with elevated $[CO_2]$ and ambient temperature. Numbers of fungal-feeding nematodes were lower in dry than in wet treatments, but only under ambient $[CO_2]$ ($[CO_2] \times H_2O$, $F_{1,16} = 6.25$, $P = 0.02$). Numbers of omni-carnivores were lower in dry than in wet treatments ($F_{1,16} = 7.07$, $P = 0.02$).

In plant-specific soils, nematodes were differentially affected by water and by plant species (Fig. 5B; Appendices D and E), as indicated by significant $H_2O \times$ species interactions for the total numbers of nematodes ($F_{1,24} = 5.33$, $P = 0.03$), for endo-parasitic nematodes ($F_{1,30} = 8.36$, $P < 0.01$), and for bacterial-feeding nematodes ($F_{1,24} = 16.33$, $P < 0.01$). Generally, we found few effects of $[CO_2]$ and temperature on numbers of nematodes in plant-specific soils. In wet treatments, the total number of nematodes was lower under *Lespedeza* than under *Festuca*; in dry treatments, the total number of nematodes was low in general and did not differ between *Lespedeza* and *Festuca* soils. Similar patterns were found for endo-parasitic plant feeders and for bacterial feeders (Fig. 5B). Numbers of endo-parasitic plant feeders were lower under elevated temperature than under ambient temperature ($F_{1,30} = 6.03$, $P = 0.02$). Root hair feeders were lower under *Lespedeza* than under *Festuca* ($F_{1,30} = 8.91$, $P < 0.01$) and, irrespective of plant species, were lower in dry than in wet treatments ($F_{1,30} = 80.10$, $P < 0.01$). Fungal-feeding nematodes were not affected by plant species. For fungal-feeding nematodes there was a significant $[CO_2] \times T \times H_2O$ interaction ($F_{1,24} = 5.20$, $P = 0.03$): overall, numbers were lower in dry than in wet treatments, but the water effect was not consistent across $[CO_2]$ and temperature treatments (Fig. 5B). Numbers of omni-carnivores were higher in soils under

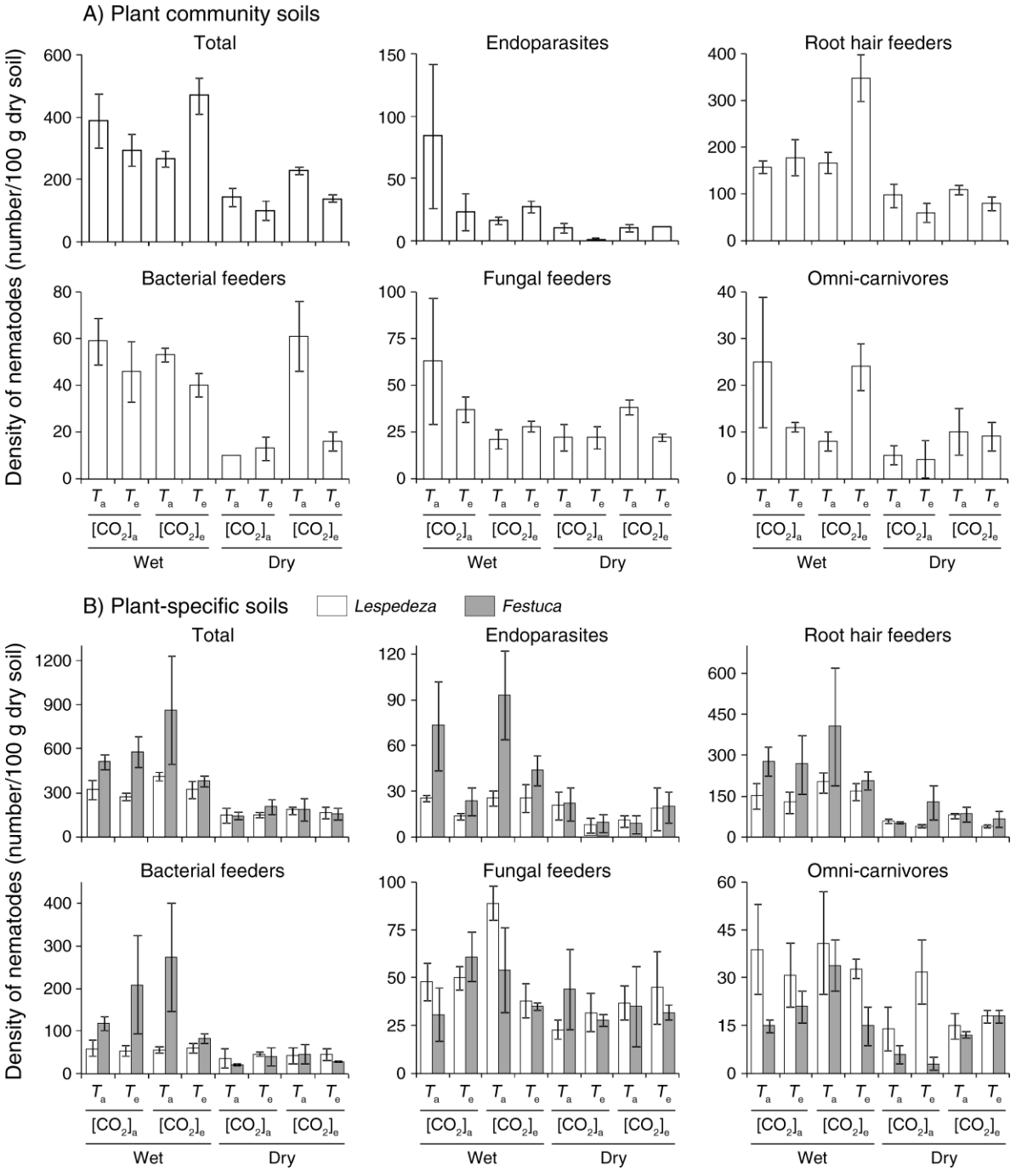

FIG. 5. Density of nematodes in (A) plant community soils and (B) plant-specific soils (i.e., soils beneath *Lespedeza* and beneath *Festuca*) under [CO_2], temperature (T), and H_2O treatments. Data are means ± SE ($n = 3$). Abbreviations are: T_a, ambient temperature; T_e, elevated temperature; $[CO_2]_a$, ambient [CO_2]; $[CO_2]_e$, elevated [CO_2].

Lespedeza than under *Festuca* ($F_{1,24} = 12.52$, $P = 0.02$) and were lower in dry than in wet treatments ($F_{1,24} = 15.26$, $P < 0.01$).

In plant-specific soils, the full RDA model, including [CO_2], temperature, water, and plant species as explanatory factors, explained >55% of the variation in nematode feeding-group composition (Table 2). Root hair feeders and bacterial feeders were the largest contributors to the community response. Most of the variation in nematode feeding groups was explained by the water treatment, as shown on the first RDA axis (Fig. 6A), followed by $H_2O \times$ species and [CO_2] $\times$ H_2O

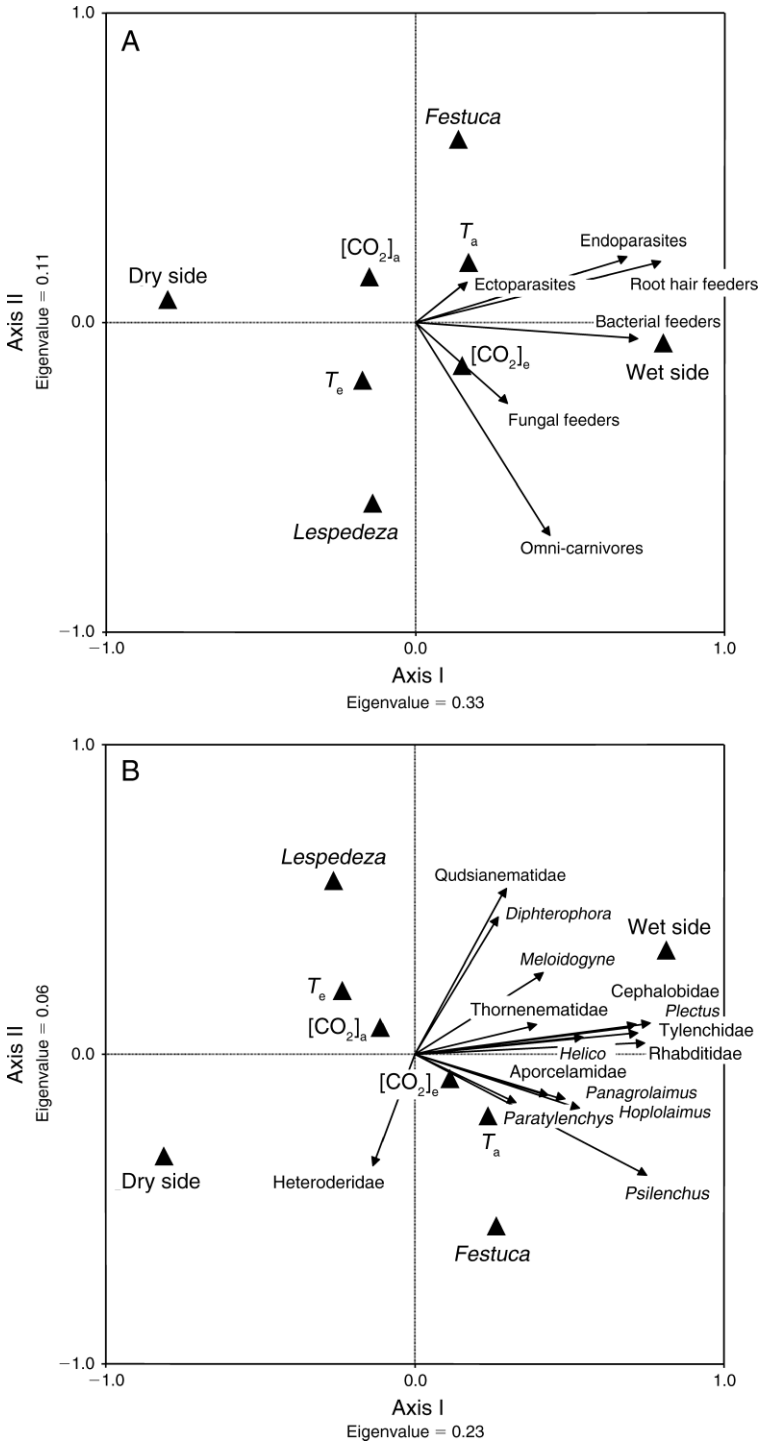

FIG. 6. Species–treatment plot resulting from the redundancy analysis of (A) nematode feeding-group composition and (B) nematode taxon composition. Treatments included are $[CO_2]$, temperature (T), H_2O, and plant species (*Lespedeza* and *Festuca*). For clarity, treatment interactions are not shown, and only the best-fitting nematode taxa are plotted in the diagram. Eigenvalues along the axes indicate the amount of explained variability in community composition. Triangles represent the centroid position of the climate-change treatments and the plant species. *Helico* is an abbreviation for *Helicotylenchus*.

interactions (Table 2). The $[CO_2] \times H_2O \times$ species interaction explained a significant amount of variation in nematode community composition (Table 2). Similar to the enzyme activities, significant species $\times$ treatment interactions indicate plant-specific changes in nematode feeding-group composition in response to the climate-change treatments (Fig. 6A).

Comparable to the nematode feeding-group composition, variation in nematode taxon composition could be best explained by water and by $H_2O \times$ species and $H_2O \times [CO_2]$ interactions. The full RDA model explained >46% of the variation in nematode taxon composition (Table 2). Root-hair-feeding *Tylenchidae* and opportunistic bacterial-feeding *Rhabditidae*, *Plectus*, and *Cephalobidae* responded most strongly to the water treatment. Omnivorous *Qudsianematidae* were associated more with *Lespedeza* than with *Festuca* (Fig. 6B). In contrast to nematode feeding-group composition, a significant amount of the variation in nematode taxon composition could be explained by the $H_2O \times T$ interaction.

The complete ANOVA results for nematode numbers are given in Appendix E.

Soil gravimetric water content

In plant community soils, gravimetric water content was, on average, 29% in wet treatments and 16% in dry treatments at the time of sampling ($F_{1,16} = 78.72$, $P < 0.01$; Appendix F). In plant community soils, gravimetric water was not significantly affected by the $[CO_2]$ or temperature treatments (Appendix G). In plant-specific soils, gravimetric water was on average 24% in wet treatments and 15% in dry treatments at the time of sampling ($F_{1,24} = 122.49$, $P < 0.01$; Appendix F). Gravimetric water content did not differ between *Lespedeza* and *Festuca* soils ($F_{1,24} = 0.66$, $P = 0.43$; Appendix F). The significant $[CO_2] \times T \times H_2O$ interaction ($F_{1,24} = 5.10$, $P = 0.03$) pointed toward somewhat higher gravimetric water in treatments with elevated $[CO_2]$ and ambient temperature. However, effects of $[CO_2]$ and temperature on gravimetric water content were small.

Discussion

Climate-change factors, i.e., elevated $[CO_2]$, warming, and altered precipitation regimes, can interactively affect soil ecosystem functioning via multiple pathways (Fig. 1). Our results show that climate-change-induced shifts in plant community composition, along with the direct effects of climate change and effects through changes in plant function, can shape the composition and functioning of soil communities.

Climate-change effects on plant community composition

Plants respond in species-specific ways to climate-change treatments, resulting in shifts in plant community composition (Diaz and Cabido 1997). Of all climate changes, altered precipitation regimes, such as anomalous droughts, probably have the strongest impact on plant community composition (Morecroft et al. 2004, Suttle et al. 2007, Knapp et al. 2008). In our multifactorial experiment, >12% of variation in plant community composition was explained by the precipitation treatment. Interactive effects of water with $[CO_2]$ and temperature were minor relative to the direct impact of the watering treatment. Reduced water shifted plant cover dominance from *Lespedeza* to *Festuca*. Total aboveground biomass was harvested at the end of 2006 and thus plant cover was low at the start of the 2007 growing season. Over the growing season, the proportional cover of *Lespedeza* increased to ~30% in dry treatments and 50% in wet treatments. In contrast, proportional cover of *Festuca* increased in dry treatments relative to wet treatments.

Plant community biomass was 80% higher in wet relative to dry treatments (P. Kardol et al., *unpublished data*); hence, community productivity in the dry treatments was strongly water limited. Generally, perennial grasses, such as *Festuca*, are adversely affected by drought (Morecroft et al. 2004); in our experiment, at the end of the growing season, shoot biomass of *Festuca* was 46% higher in wet relative to dry treatments (P. Kardol et al., *unpublished data*). Therefore, increase in *Festuca* proportional cover in dry treatments toward the end of the season should not be attributed to direct effects of the precipitation treatment, but to decreased competition from neighboring *Lespedeza* plants. In wet treatments, *Lespedeza* had the greatest amount of biomass relative to other species; this is most likely due to its extensive root system that may enable high water uptake capacity.

Importantly, structural and chemical differences between the N_2-fixing sub-shrub *Lespedeza* and the C_3 grass *Festuca* indicate that shifts in their proportional cover have far-reaching ecological consequences. In our study, we focused on consequences for soil ecosystem functioning, but structural and chemical changes in plant communities in response to climate change can also affect aboveground communities of insect herbivores and their predators (e.g., Schadler et al. 2007, Villalpando et al. 2009).

Climate-change effects on soil ecosystem functioning

In our multifactorial experiment, enzyme activities and nematodes were much stronger impacted by the water treatment than by elevated $[CO_2]$ or warming. Responses of enzyme activities to the water treatment depended upon the compounds they assist with breaking down. Activity of enzymes involved in degradation of recalcitrant organic compounds (e.g., lignin) was generally lower in dry relative to wet treatments. This response to the water treatment could be due to reduced enzyme production as a result of soil microbial moisture stress or to direct effects of low moisture on enzyme activity (Toberman et al. 2008). Alternatively, in wet treatments, labile organic compounds are depleted

quickly, leaving behind a largely recalcitrant C pool (Conant et al. 2008). The activity of cellobiohydrolase, an enzyme involved in degradation of a labile organic compound (i.e., cellulose), was higher in dry than in wet treatments; the reason why remains speculative. Higher activity of enzymes involved in degrading labile compounds could be associated with higher root biomass and, hence, the increased availability of labile, root-derived compounds to soil microorganisms (Henry et al. 2005); however, preliminary analyses of long-term mini-rhizotron data do not show substantial changes in overall root biomass in response to the water treatment in our experiment (C. Iversen, *unpublished data*).

Similar to enzyme activities, nematode response to the water treatment depended on their functional role in the decomposition process. However, overall, numbers of nematodes were lower in dry than in wet treatments. Except for endo-parasitic plant feeders, nematodes live in water films between soil particles, making them highly dependent on soil gravimetric water content for their mobility and survival (Warwick 1984). Gravimetric water content of the soil samples from the dry treatments was >10%, which might be sufficient for nematodes to survive and reproduce; however, during the hot summer months, soil volumetric water content in dry treatments could drop to below 5%. Nematode abundances in the soil samples we collected in October may have reflected soil moisture conditions from preceding months. Interestingly, decline in numbers of nematodes in dry treatments was generally moderated by elevated [CO_2] and generally lower under ambient temperature than under elevated temperature in plant community soils, though not in plant-specific soils. This suggests that moderation of water by elevated [CO_2] and warming can be outweighed by plant-specific effects on nematode numbers. Such plant-specific effects on soil ecosystem responses to climate change have been largely overlooked in previous studies (e.g., Henry et al. 2005).

Plant-specific effects on soil (micro)-organisms and their functioning (e.g., the activities of the enzymes they excrete) should be attributed to the quantity and quality of organic compounds plants put into the soil and to plant-specific effects on soil microhabitat conditions (e.g., Waldrop and Firestone 2006, Viketoft et al. 2009). We showed that activity of enzymes involved in degradation of orthophosphate, sulphur, cellulose, and chitin were lower in soils under *Lespedeza* than in soils under *Festuca*. Reduced enzyme activities in soils under *Lespedeza* relative to soils under *Festuca* could suggest a negative effect of *Lespedeza* on microbial activity, which might have resulted from high concentrations of polyphenolics in organic residues from *Lespedeza* (Langdale and Giddens 1967). However, activities of other enzymes, including enzymes involved in the degradation of lignin, were similar in soils under *Lespedeza* and *Festuca*. High availability of lignin in soils under the woody sub-shrub *Lespedeza* may have stimulated microorganisms involved in lignin degradation, hence, compensating for a reduction in overall microbial activity. Overall, the enzyme activities indicated slower rates of nutrient and C cycling in soils beneath *Lespedeza* than beneath *Festuca* and suggest that shifts in plant community composition could function as an enzymic "latch" mechanism controlling soil nutrient and C stocks (sensu Freeman et al. 2001).

The suggestion of slower nutrient and C-cycling rates beneath *Lespedeza* was supported by the nematode response, but only in the wet treatment. Numbers of nematodes were consistently low and were not significantly affected by plant species in dry treatments. In contrast, nematodes were responsive to the plant species in wet treatments, and the responses differed among feeding groups. Plant-associated nematodes in soils under *Lespedeza* could have been inhibited by the chemical composition (e.g., high levels of toxins) or the physical structure (e.g., woodiness) of *Lespedeza* roots. Lower numbers of bacterial-feeding nematodes under *Lespedeza* could have been due to low resource availability (sensu Griffiths et al. 1992); the low rates of enzyme activities beneath *Lespedeza* indicate that there might also be lower microbial biomass. Similar numbers of fungal-feeding nematodes in soil beneath *Lespedeza* and *Festuca* may indicate that fungal biomass did not differ among these soils. The differential responses of bacterial- and fungal-feeding nematodes to the plant species indicate that in wet soils, decomposition is more fungal-based (slow cycle) in soils beneath *Lespedeza* and more bacterial-based (fast cycle) in soils beneath *Festuca*.

Interestingly, in plant community soils, bacterial-feeding nematodes were more sensitive to reduced precipitation than fungal-feeding nematodes, indicating slower rates of nutrient and C cycling under dry conditions. We would have predicted the opposite, as higher proportional cover of *Lespedeza* in wet treatments should lead to slower rates of nutrient and C cycling. These data suggest that the soil samples we collected to represent the overall contribution of the plant community did not accurately represent the proportional cover of the dominant plant species. These results illustrate that when soils are collected from relatively few areas in a study system to represent the overall ecosystem response, they may not accurately reflect the integrated soil response.

In general, we found that climate changes influence enzyme activities more strongly in plant-specific soils than in plant community soils. If plant species have opposing effects on soil microorganisms and the enzymes they excrete, it could be that plant-specific climate-change effects have canceled each other out in plant community soils, resulting in no net effect. This could suggest that plant-specific climate-change effects on soil ecosystem functioning are of minor importance at the community level. However, this is not a likely scenario when climate change concurrently affects plant

community composition (as our result show). Instead, weak enzyme responses to the climate-change treatments in plant community soils could well be related to the spatial configuration of the soil samples. Bulk soils collected between plant species may have contained proportionally less rhizosphere soil than plant-specific soils, diluting the response of individual plant species; microbial activity is generally higher in rhizosphere soils than in bulk soils (Mukerji et al. 2006), and enzyme activities decrease with distance from the plant (Miniaci et al. 2007).

On the contrary, most nematodes do not directly rely on rhizosphere products as food source and exhibit patchy distributions at larger spatial scales than soil microorganisms (Ettema and Wardle 2002); their abundance was similar in plant community soils and in plant-specific soils. This could suggest that climate-change effects on soil nematodes are less dependent on effects via changes in individual plant function (Fig. 1, pathway 2) and more dependent on direct effects of climate change (Fig. 1, pathway 1). We did, however, find significant interactions of climate change and plant species on most of the nematode feeding groups and on nematode community composition, indicating that climate-change effects via changes in plant community composition (Fig. 1, pathway 3) do contribute to the net climate-change effects on soil nematode communities.

Differences in enzyme activities and nematodes between plant community soils and plant-specific soils could have been confounded by differences in soil climatic conditions associated with the difference in sampling date. However, across treatments, mean daily soil temperature in the open-top chambers on the day plant community and plant-specific soils were collected was about the same (12.7°C and 12.5°C, respectively). In the wet treatments, soil moisture content was 5% higher in the plant community soils than in the plant-specific soils. In the dry treatments, soil moisture content did not differ between plant community soils and plant-specific soils. Based on soil moisture data we would expect that, in wet treatments, enzyme activities and numbers of nematodes were higher in plant community soils than in plant-specific soils. As we generally found the opposite, we do not think that the difference in sampling date significantly contributed to differences between plant community soils and plant-specific soils.

Synthesis

Differential responses of enzymes involved in degradation of recalcitrant and labile organic compounds and of nematode feeding groups to changes in precipitation regime may have important consequences for the distribution of C among transient and more stable soil C pools, potentially promoting C sequestration under dry conditions (Tate and Ross 1997, Freeman et al. 2001). However, our results show that drought-related C sequestration could be moderated when changes in precipitation regimes concurrently affect plant dominance patterns, promoting plant species associated with high C-cycling rates. In other words, soil ecosystem responses to climate changes could be offset or reversed when climate changes result in plant community composition shifts (Fig. 1, pathway 3). Accurate assessment of climate-change impacts on soil ecosystem functioning requires incorporation of the concurrent changes in plant function, distribution, and community composition. Future research should focus on improving our understanding of the manner in which climate-change-induced shifts in plant distributions and dominance patterns and plant-specific effects on soil properties interactively affect soil ecosystem function. Predicting long-term (soil) ecosystem response and feedback to climate change requires integration of ecosystem ecology and plant biogeography.

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APPENDIX A

Proportional plant species cover across wet and dry treatments (*Ecological Archives* E091-056-A1).

APPENDIX B

Enzyme activities in plant community soils and in plant-specific soils (*Ecological Archives* E091-056-A2).

APPENDIX C

Results from ANOVA testing the effects of climate-change treatments on extracellular enzyme activities in plant community soils and in plant-specific soils (*Ecological Archives* E091-056-A3).

APPENDIX D

Density of nematodes in plant community soils and in plant-specific soils (*Ecological Archives* E091-056-A4).

APPENDIX E

Results from ANOVA testing the effects of climate-change treatments on total number of nematodes and numbers of nematodes per feeding group in plant community soils and in plant-specific soils (*Ecological Archives* E091-056-A5).

APPENDIX F

Soil moisture content in plant community soils and in plant-specific soils (*Ecological Archives* E091-056-A6).

APPENDIX G

Results from ANOVA testing the effects of the climate-change treatments on soil moisture content in plant community soils and in plant-specific soils (*Ecological Archives* E091-056-A7).