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Short Communication

Elevated CO2 and warming shift the functional composition of soil nematode communities in a semiarid grassland

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Abstract
Climate change can alter soil communities and functions, but the consequences are uncertain for most ecosystems. We assessed the impacts of climate change on soil nematodes in a semiarid grassland using a 7-year, factorial manipulation of temperature and [CO2]. Elevated CO2 and warming decreased the abundance of plant-feeding nematodes and nematodes with intermediate to high values on the colonizer-persister scale (cp3-5), including predators and omnivores. Thus, under futuristic climate conditions, nematode communities were even more dominated by r-strategists (cp1-2) that feed on bacteria and fungi. These results indicate that climate change could alter soil functioning in semiarid grasslands. For example, the lower abundance of plant-feeding nematodes could facilitate positive effects of elevated CO2 and warming on plant productivity. The effects of elevated CO2 and warming on nematode functional composition were typically less than additive, highlighting the need for multi-factor studies.

Nematodes are a morphologically and functionally diverse group of soil organisms (Bongers and Bongers, 1998; Ferris, 2010; Ferris et al., 2001; Neher, 2010; Yeates et al., 1993), so shifts in nematode community composition can provide clues about the sensitivity of soil food webs and soil functions to climate change. However, the impacts of climate change on nematode abundance have been idiosyncratic across studies, ranging from positive to negative for unknown reasons. Even when focusing on specific nematode functional groups, such as plant-feeders, the impacts of climate change on nematode abundance vary considerably across studies (A’Bear et al., 2014; Ayres et al., 2008; Blankinship et al., 2011; Cesár et al., 2015; Ferris et al., 2012). The lack of predictability of nematode responses to climate change likely reflects three sources of variation among studies: i) biogeographic variation in how climate change influences soil abiotic conditions (e.g., moisture) and the basal resources of soil food webs, including roots, bacteria, and fungi (García-Palacios et al., 2015), ii) variation in the extent to which various factors regulate soil food web structure (e.g., abiotic vs. biotic factors, top-down vs. bottom-up factors, indirect vs. direct effects of climate change) (Kardol et al., 2010; Shao et al., 2015), and iii) variation in the taxonomic and functional resolution of nematode identification (Cesarz et al., 2015; Neher and Weich, 2013). Thus, additional studies are required to generate hypotheses and better understand the impacts of climate change on soil nematodes. Multi-factor studies are especially needed because of their rarity and potential for interactions among multiple aspects of climate change (e.g., warming and elevated CO2; Eisenhauer et al., 2012). There are only two reports of the combined, in situ effects of elevated CO2 (eCO2) and warming on nematode communities, both for rice paddies in Asia (Chen et al., 2015; 2016).
relative abundance

Experimental treatment

Fig. 1. Abundance of nematode functional groups characterized by trophic position (left) and life-history traits (the colonizer-persister scale; right). Bars show treatment means (±SE, n = 5). The cp scale ranks nematodes along a spectrum from those with r-selected traits (cp1), e.g., short generation times and high fecundity, to those with K-selected traits (cp5). Plant-feeding nematodes are not included in the results shown for cp groups because their life-history strategies might not be comparable to other trophic groups (Bongers, 1990). The relative abundance of cp1 nematodes was very low (~2% in all but one plot), so the sum of cp1 and cp2 nematodes are shown. Similarly, the relative abundance of predators was very low (~2% in all but one plot), so the sum of predators and omnivores are shown. **Bold print** indicates model terms with P < 0.05 and **italic print** indicates model terms with 0.05 < P < 0.1. The treatment interaction term is also shown in normal print if 0.1 < P < 0.2 because in factorial designs with low statistical power, risk of Type II errors is likely much greater than that of Type I errors (Smith et al., 2002) and the interpretation of main effects is conditional upon the interaction (Stehman and Meredith, 1995). When the interaction term had P < 0.2, treatment means labelled with different letters were marginally significantly different according to post-hoc Tukey tests (α = 0.1). *Abundance was estimated by multiplying the total number of nematode individuals in each plot by the relative abundance of each functional group (derived from identification of ~100 nematodes per plot).

Here, using a factorial field experiment, we describe the in situ impacts of eCO2 and warming on the nematode community in a semi-arid, mixed-grass prairie in Wyoming, U.S.A. Mixed-grass prairies are the most widespread grassland type in North America (Samson et al., 2004). Nematodes could play an important role in shaping the functions of mixed-grass prairies because grasslands typically have high nematode densities and, for example, plant productivity is sensitive to shifts in nematode density (Bardgett et al., 1999; Hunt et al., 1987; Hunt and Wall, 2002; Ingham and Detling, 1990; Stanton, 1988). Reports from this experiment in Wyoming show that warming and eCO2 have influenced abiotic soil conditions, including temperature, moisture, and nutrient pools, as well as the basal parts of soil food webs, including roots and microbes (Carrillo et al., 2014, 2012; Dijkstra et al., 2012, 2010; Mueller et al., 2016). Given these shifts in resource availability and microclimate due to eCO2 and warming, we expected associated shifts in nematode abundance and community composition, i.e., we tested the null hypothesis that eCO2 and warming do not impact nematodes. The eCO2 treatment increased [CO2] to ~600 ppm using Free-Air CO2 Enrichment (FACE) technology and was implemented during all seasons. The warming and eCO2 treatments were maintained for 7 and 8 years, respectively, with 5 replicates per treatment (2006–2013) (LeCain et al., 2015; Morgan et al., 2011).

We sampled nematodes during the experiment’s final year. In late July, which is typically within a few weeks of peak plant production aboveground, three soil cores (3 cm diameter; 15 cm deep) were collected for nematode extraction from each experimental plot. Soils were composited at the plot level (n = 20) and
refigerated (<48 h) prior to extraction. Nematodes were extracted over 72 h using Baermann funnels (Baermann, 1917) and preserved in a 5% formalin solution. For each sample, nematodes were counted using an inverse Leica DMI 4000B light microscope at 50× magnification and at least 100 individuals were randomly identified at 400× magnification following Bongers (1988); adults were identified to genus-level and most juveniles were identified to family-level. We identified nematode adults from 44 genera and juvenile nematodes from six families. Nematode taxa were then arranged into trophic groups (Bongers and Bongers, 1998; Okada et al., 2005; Yeates et al., 1993), ordered according to the colonization–persistence gradient (cp values) (Bongers, 1990; Bongers and Bongers, 1998), and assigned to functional guilds by combining trophic groups with cp values (Bongers and Bongers, 1998; Ferris et al., 2001) (Supplemental Table 1). We evaluated the role of cp values separately for plant-feeding nematodes (parasitic) and other nematodes (non-parasitic) because the life-history strategies of plant-feeding nematodes might not be comparable to other trophic groups (Bongers, 1990). We used mixed-models to evaluate the significance of treatment effects and interactions (fixed effects), while accounting for the distribution of plots across two blocks (random effect) with slightly different soil types. When treatment interaction terms had $P < 0.2$ (sensu Stehman and Meredith, 1995), we used post-hoc Tukey tests to compare treatment means using $\alpha = 0.1$.

Elevated CO$_2$ and warming altered nematode community composition (Fig. 1). For several nematode functional groups, negative treatment effects were more apparent for absolute abundance than for relative abundance, because total nematode abundance was lower in all treated plots compared to the controls (11.4 nematodes per g of soil ±1.2 SE and 17.8 nematodes per g of soil ±3.1 SE, respectively; $P > 0.1$). Both eCO$_2$ and warming tended to decrease the abundance of three nematode functional groups (Fig. 1), including plant-feeding nematodes, predators plus omnivores, and non-parasitic nematodes with intermediate to high cp values (cp3 to cp5, where high values reflect a K-selected strategy; predators and omnivores were assigned cp values of 4 or 5). Consequently, the relative abundance of other functional groups of nematodes tended to increase in response to eCO$_2$ and warming, especially bacteria- and fungi-feeding nematodes that are on the ‘colonizer’, r-selected end of the cp scale (cp1 and cp2; Fig. 1). More than 90% of plant-feeding nematodes were characterized as cp2 or cp3 (Supplemental Table 1), and these two groups of plant-feeders had similar responses to the treatments. The relative abundance of some groups of nematodes was more sensitive to eCO$_2$ (plant-feeding and bacteria-feeding nematodes), while other groups were more sensitive to warming (non-parasitic cp3 and cp4 nematodes; Fig. 1). There was no evidence that the treatments influenced various indices of nematode diversity or relative abundance of the fungal or bacterial decomposition pathways (data not shown).

The treatment effects were less than additive for several groups of nematodes, reflecting potential CO$_2$ × warming interactions (Fig. 1). For plant-feeding nematodes, predators plus omnivores, and non-parasitic nematodes with cp3 or cp4, if the negative effects of eCO$_2$ and warming alone were additive, the expected mean abundance of these groups in the eCO$_2$+warming treatment would be zero; yet, their abundance in the combined treatment was similar to that in the eCO$_2$ alone and warming alone treatments.
warming and eCO2 tended to have positive, but sub-additive effects on the number and length of fine roots (Carrillo et al., 2014; Mueller et al., unpublished) and the amount of C and N in microbial biomass (Carrillo et al., 2012; Dijkstra et al., 2010). Also, the relative abundance of bacterial-feeding and plant-feeding nematodes was correlated with the concentration of a single PLFA attributed to gram negative bacteria (Fig. 3), which can be abundant in the rhizosphere (Griffiths et al., 1999). Finally, Suseela et al. (in review) observed positive, and sometimes sub-additive, effects of eCO2 and warming on the amount of suberin and individual suberin monomers in plant roots. If these plant biomolecules inhibit plant-feeding nematodes (Biederman and Boutton, 2009; Holbein et al., 2016), this result could help explain the negative, sub-additive effects of eCO2 and warming on the abundance of plant-feeding nematodes (Fig. 1). In turn, the diminished abundance of plant-feeding nematodes could have contributed to observed positive responses of plant productivity, above and below-ground, to both eCO2 and warming (Carrillo et al., 2014; Mueller et al., 2016).

Collectively, these results suggest the impacts of climate change on nematodes might be largely indirect and mediated from the “bottom-up” by plants and microbes.

Additional information was gained by classifying nematodes into functional guilds defined by both trophic position and life history (Fig. 2). Consistent with expectations for natural grasslands (Ferris et al., 2001), the nematode communities in control plots had a relatively high Structure Index, reflecting abundant trophic links and high abundance of predators and omnivores within the nematode community; this structure was diminished by the treatments, particularly by warming alone (Fig. 2). The mean Enrichment Index, reflecting the abundance of opportunistic bacteria- and fungifeeding nematodes that respond to resource enrichment, was relatively low and similar across control and treatment plots. However, due to a few higher enrichment values in treated plots, the control plots showed less variability in the Enrichment Index (Fig. 2). According to the original interpretation of these functional indices (Ferris et al., 2001), by reducing the number of trophic links within the nematode community and increasing the relative abundance of the basal components of the soil food web (particularly bacteria- and fungi-feeding nematodes), the future climatic conditions implemented in the PHACE experiment have induced a shift toward a soil food web that is “degraded” and “stressed”, and possibly less regulated by top-down effects.

The shifts in nematode functional composition we observed suggest that, for the expansive mixed-grass prairie of North America, climate change could have significant impacts on below-ground food webs and functions (e.g., decomposition, respiration, nutrient cycling). To better predict the impacts of climate change on nematode communities and soil functions across ecosystems, our results and those of other recent studies (Cesarz et al., 2015; Kardol et al., 2010; Neher and Weicht, 2013; Thakur et al., 2014) suggest that: i) more factorial studies should be conducted (e.g., CO2 × warming), and ii) nematode abundance should be measured for functional groups defined by trophic level and life history.

Author contributions

DMB and EP helped design and conduct the experiment; KEM analyzed the data and wrote the first draft of the manuscript, with input and revisions provided by all authors. Except for KEM and NE, authors are listed in alphabetical order.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.08.005.

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