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Nematode functional guilds, not trophic groups, reflect shifts in soil food webs and processes in response to interacting global change factors

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ABSTRACT

Soils store ~80% of global terrestrial organic carbon and alterations in fluxes into and out of this pool may interact with ongoing climate change. Belowground food webs drive soil C dynamics, but little is known about their responses to co-occurring global change agents. We investigated open-air experimental grassland communities at ambient and elevated atmospheric CO_2 concentration, ambient and enriched nitrogen input, and ambient and reduced summer precipitation to evaluate how these agents interactively affect soil nematodes, which are often used as an indicator group for soil food web structure and soil health. The aim of the study was to elucidate the response of the functional diversity of soil nematodes to changing environmental conditions by using nematode functional guilds and indices as indicators.

The results suggest that nematode functional guilds surpass nematode trophic groups as soil indicators, suggesting that more detailed data on nematode community structure is essential to capture functional changes in response to environmental change. For instance, the density of opportunistic fungal feeders increased due to N addition with the response being more pronounced at elevated CO_2, whereas densities of sensitive fungal-feeders were increased at ambient N and elevated CO_2, illustrating opposing responses within one trophic group. Opportunistic bacterial feeders increased at elevated N, but did not respond to other environmental factors studied. Root-feeding Longidoridae were significantly reduced at elevated CO_2 and elevated N compared to ambient conditions, whereas other plant feeders were little affected by the manipulations. Predacious nematodes were less abundant at elevated N, and the Structure Index (which indicates food web structure) suggested reduced top-down forces and simplified soil food webs, although omnivores did not vary significantly. Elevated CO_2 buffered the effect of reduced precipitation on the Enrichment Index (which indicates increased resource availability) and the Channel Index (which indicates changes in decomposition channel) probably due to reduced stomatal conductance at elevated CO_2. Further, the results suggest that the decomposer community switched from a bacterial-dominated to a fungal-dominated system at elevated N, indicating shifts in the microbial community as well as in the functioning of belowground food webs. Overall, the studied global change agents interactively and differentially affected functional guilds of soil nematodes, suggesting complex changes in soil processes. We highlight that detailed information on the functional guilds of nematodes is likely necessary to fully understand alterations in soil food webs and related processes due to global environmental change.

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Introduction

Human activities lead to changes in atmospheric CO_2 concentrations, nitrogen (N) deposition, and precipitation regimes with considerable impacts on ecosystem functioning (IPCC 2007). These global change agents are acting in concert, and understanding their interactive effects is crucial to predict the consequences for ecosystem functions and services (Reich et al. 2006a). Typically, in terrestrial ecosystems >90% of the biomass produced by plants enters the dead organic matter pool forming the basis of the decomposer system (Schlesinger and Andrews 2000). Thus, understanding interactions between plants and decomposers is of high importance, especially as the balance between carbon sequestration and carbon loss depends on those interrelationships (Gessner et al. 2010) as well as on interactions between global change agents (Zaehle 2013).

Since the industrial revolution, CO_2 concentrations in the atmosphere have increased from approximately 270 ppm to 380 ppm in 2005 and presumably will reach 550 ppm by the year 2050 (IPCC 2007; Rogelj et al. 2012). Higher atmospheric CO_2 concentrations significantly impact plant physiological processes. At least three responses are relevant to the decomposer system. Most prominent is the increase in plant carbon (C) acquisition, which leads to both greater biomass production (Ainsworth and Long 2005) and greater inputs of labile C forms to the soil (Adair et al. 2011). Also, increasing C acquisition is usually associated with a larger C-to-N ratio of live plant tissue, and, therefore, reduced tissue quality for consumers (Körner 2000). These plant responses have cascading effects on both aboveground (Lau and Tiffin 2009) and belowground consumers (Blankinship et al. 2011), the latter representing important drivers of soil processes, such as organic matter decomposition and nutrient mineralization. Belowground responses to higher plant biomass production and rhizodeposition under elevated atmospheric CO_2 can either increase C loss by increasing bottom-up forces leading to increased decomposition or enhance C sequestration when top-down forces counter bottom-up forces (Wardle et al. 1998; Schulze and Freibauer 2005). This balance has major implications for ecosystem feedback effects on atmospheric CO_2 concentrations and therefore on the global C cycle, and may depend on other co-occurring global change agents, such as N inputs (Hoeksema et al. 2000; Chung et al. 2007).

Nitrogen is a key nutrient in terrestrial ecosystems (LeBauer and Treseder 2008) and crucially determines processes, such as decomposition, mineralization and nitrification (Swift et al. 1979; Parton et al. 2007). The previously reported effects of N addition on different belowground processes have been positive, negative and neutral, reflecting that N regimes in soils are poorly understood and may be context-dependent (Knorr et al. 2005; Keeler et al. 2008). N fertilization often increases plant productivity but also decreases plant and soil animal diversity by increasing the abundance of already dominant species (Clark and Tilman 2008; Reich 2009; Eisenhauer et al. 2012). Elevated N availability can decrease rhizodeposition (Dijkstra et al. 2005; Högberg et al. 2010) with neutral to negative effects on soil microorganisms and higher trophic levels of soil organisms (Eisenhauer et al. 2012). As most terrestrial ecosystems are N-limited, fertilization and atmospheric N deposition may induce unexpected CO_2 responses with poorly understood consequences for the belowground system and ecosystem functioning (Reich et al. 2006b). Previous studies on soil biota found interactive effects of increased atmospheric CO_2 concentrations and N fertilization (Hoeksema et al. 2000; Hu et al. 2001; Eisenhauer et al. 2012). However, long-term responses of the belowground system remain little understood (Bardgett and Wardle 2010), though they are important as ecosystems often respond slowly to environmental changes (Kuzyakov and Gavrichkova 2010).

In addition to altered CO_2 and N levels, climate is projected to change with altered precipitation regimes (IPCC 2007; Kerr 2007). Soil moisture and related biotic and abiotic parameters are important driving forces for soil processes (Kardol et al. 2010). Drought has mostly negative effects on soil fauna by decreasing directly their reproduction and development (Lindberg et al. 2002) or indirectly by changing the composition and biomass of microorganisms (Hawkes et al. 2011) and plants (Kardol et al. 2010). In addition, responses to changes in soil moisture regimes depend on the plant community (Gross et al. 2008). Soil moisture may interact with CO_2 and N availability because elevated CO_2 levels often increase soil water content and N content increases with higher soil moisture (Körner 2000; Zhang and Wienhold 2002); therefore, complex interactions in soil processes and involved soil biota are likely. Recently, Reich et al. (2014) showed highest biomass production at elevated CO_2, elevated N and ambient rain (not removed) and revealed complex relationships that, e.g., a lacking CO_2 effect may be due to other limiting nutrients and moisture conditions. Most previous studies were based only on short-term experiments and separately investigated global change agents (Blankinship et al. 2011). Although these studies provided important insights into the mechanisms underlying main effects, interactions between co-occurring global change agents have to be considered to get more realistic predictions of future changes.

One promising approach to detect changes in soil processes is the investigation of soil food web structure, exemplified by the composition of functional guilds of nematodes (Bongers 1990; Yeates et al. 1993; Ferris et al. 2001). As nematodes have diverse feeding behaviors and life strategies and play a key role in soil food webs, they function as important indicators for ecosystem processes (Ferris 2010; Yeates 2010). Functional grouping of nematodes provides important information to detect changes in soil processes by considering distinct feeding strategies, e.g., bacterial or fungal-feeding in combination with their responses (tolerance vs. sensitivity) to environmental changes. In addition, nematode-based indices allow the evaluation of ecosystem nutrient status (enriched vs. depleted), structure of the soil food web (complexity vs. simplicity), and the relevance of decomposition channels (bacterial vs. fungal) (Ferris et al. 2001).

We used a well-established global change experiment in grassland (BioCON; Reich et al. 2001a,b,c) to explore interactive effects of elevated atmospheric CO_2, N deposition, and reduced summer precipitation (Reich et al. 2014) on soil nematode communities. The BioCON experiment had been ongoing for 13 years by the time of this study, and results therefore are likely not biased by transient effects caused by the establishment of the experiment (Reich et al. 2012). In a recent study, Eisenhauer et al. (2012) investigated the effects of elevated CO_2, elevated nitrogen, and drought on soil organisms, i.e., protozoa, mites, springtails, thysanoptera and also on nematodes by arranging them in trophic groups, i.e., bacterial feeders, fungal feeders, plant feeders, omnivores, and predators. They found altered soil communities, probably due to treatment-induced changes in rhizodeposition. The present study aims to reveal changes in soil processes by arranging nematodes into functional guilds using the approach by Ferris et al. (2001). This approach accounts for different life history strategies in each trophic group, therefore, increasing the resolution of the data and providing novel insights into the functional changes in soil food webs. For instance, opportunistic fungal-feeding nematodes are favored by high nutrient supply and are tolerant to environmental stress, whereas sensitive fungal-feeding nematodes respond negatively to disturbance (Ferris et al. 2001). This can result in two completely different responses within one trophic group, and the coarse aggregation into trophic groups will not be able to detect such important functional changes (Okada and Harada 2007; Neher and Weicht 2013).