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

Simone Cesarz^{*a,b,c}, Peter B. Reich^{d,e}, Stefan Scheu^a, Liliane Ruess^f, Matthias Schaefer^a
and Nico Eisenhauer^{b,c}

^a J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University
Göttingen, Berliner Straße 28, 37073 Göttingen, Germany

^b German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,
Deutscher Platz 5e, 04103 Leipzig, Germany

^c Institute of Biology, University of Leipzig, Johannisallee 21, 04103 Leipzig, Germany

^d Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue N.,
St. Paul, MN 55108, USA

^e Hawkesbury Institute for the Environment, University of Western Sydney, Penrith,
NSW, 2751, Australia

^f Institute of Biology, Humboldt University Berlin, Philippstr. 13, 10115 Berlin,
Germany

Running title: Global change and soil nematode communities

*Corresponding author: Simone.Cesarz@idiv.de

Phone: +49 341 9733174

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 CO₂ 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 CO₂, whereas densities of sensitive fungal-feeders were increased at ambient N and elevated CO₂, 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 CO₂ 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 CO₂ 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 CO₂. 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.

Key-words: nematodes, food web complexity, global change, grassland, soil processes, taxonomical resolution

Introduction

Human activities lead to changes in atmospheric CO₂ 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

71 depends on those interrelationships (Gessner et al., 2010) as well as on interactions
72 between global change agents (Zaehle, 2013).

73 Since the industrial revolution, CO₂ concentrations in the atmosphere have increased
74 from approximately 270 ppm to 380 ppm in 2005 and presumably will reach 550 ppm
75 by the year 2050 (IPCC, 2007; Rogelj et al., 2012). Higher atmospheric CO₂
76 concentrations significantly impact plant physiological processes. At least three
77 responses are relevant to the decomposer system. Most prominent is the increase in
78 plant carbon (C) acquisition, which leads to both greater biomass production
79 (Ainsworth and Long, 2005) and greater inputs of labile C forms to the soil (Adair et al.,
80 2011). Also, increasing C acquisition is usually associated with a larger C-to-N ratio of
81 live plant tissue, and, therefore, reduced tissue quality for consumers (Körner, 2000).

82 These plant responses have cascading effects on both aboveground (Lau and Tiffin,
83 2009) and belowground consumers (Blankinship et al., 2011), the latter representing
84 important drivers of soil processes, such as organic matter decomposition and nutrient
85 mineralization. Belowground responses to higher plant biomass production and
86 rhizodeposition under elevated atmospheric CO₂ can either increase C loss by
87 increasing bottom-up forces leading to increased decomposition or enhance C
88 sequestration when top-down forces counter bottom-up forces (Schulze and Freibauer,
89 2005; Wardle et al., 1998). This balance has major implications for ecosystem feedback
90 effects on atmospheric CO₂ concentrations and therefore on the global C cycle, and may
91 depend on other co-occurring global change agents, such as N inputs (Chung et al.,
92 2007; Hoeksema et al., 2000).

93 Nitrogen is a key nutrient in terrestrial ecosystems (LeBauer and Treseder, 2008) and
94 crucially determines processes, such as decomposition, mineralization and nitrification
95 (Parton et al., 2007; Swift et al., 1979). 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 (Keeler et al., 2008; Knorr et al., 2005). 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 CO₂ 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 CO₂ concentrations and N fertilization (Eisenhauer et al., 2012; Hoeksema et al., 2000; Hu et al., 2001). 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 CO₂ 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 CO₂ and N availability because elevated CO₂ levels often increase soil water content and N content

121 increases with higher soil moisture (Körner, 2000; Zhang and Wienhold, 2002);
122 therefore, complex interactions in soil processes and involved soil biota are likely.
123 Recently, Reich et al., (2014) showed highest biomass production at elevated CO₂,
124 elevated N and ambient rain (not removed) and revealed complex relationships that,
125 e.g., a lacking CO₂ effect may be due to other limiting nutrients and moisture
126 conditions.
127 Most previous studies were based only on short-term experiments and separately
128 investigated global change agents (Blankinship et al., 2011). Although these studies
129 provided important insights into the mechanisms underlying main effects, interactions
130 between co-occurring global change agents have to be considered to get more realistic
131 predictions of future changes.
132 One promising approach to detect changes in soil processes is the investigation of soil
133 food web structure, exemplified by the composition of functional guilds of nematodes
134 (Bongers, 1990; Ferris et al., 2001; Yeates et al., 1993). As nematodes have diverse
135 feeding behaviours and life strategies and play a key role in soil food webs, they
136 function as important indicators for ecosystem processes (Ferris, 2010; Yeates, 2010).
137 Functional grouping of nematodes provides important information to detect changes in
138 soil processes by considering distinct feeding strategies, e.g., bacterial or fungal-feeding
139 in combination with their responses (tolerance vs. sensitivity) to environmental changes.
140 In addition, nematode-based indices allow the evaluation of ecosystem nutrient status
141 (enriched vs. depleted), structure of the soil food web (complexity vs. simplicity), and
142 the relevance of decomposition channels (bacterial vs. fungal) (Ferris et al., 2001).
143 We used a well-established global change experiment in grassland (BioCON; Reich et
144 al., 2001ab, Reich et al. 2006) to explore interactive effects of elevated atmospheric
145 CO₂, 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 CO₂, 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 (Neher and Weicht, 2013; Okada and Harada, 2007).

We hypothesized that elevated CO₂, elevated N, reduced precipitation, and their interactions differently affect nematode functional guilds due to functional differences within one trophic group. In more detail, we assume opportunistic nematodes to benefit from increased resource availability via increased plant biomass being highest at the combination of elevated CO₂, elevated N and ambient summer precipitation as well as increased rhizodeposition caused by elevated CO₂ but to be less affected by negative effects caused by N fertilization and reduced precipitation. Generally, we expect

171 nematode functional guilds to be strongly influenced by interactions between the three
172 global change agents being unpredictable from single factor effects.

173

174 **Material and Methods**

175 Location and experimental design

176 The study was conducted within the framework of the BioCON experiment (short for
177 *Biodiversity, CO₂ and N*) at Cedar Creek in Minnesota, USA (Reich et al., 2001a; Reich
178 et al., 2001b). The site is situated on an N limited glacial outwash sand plain with soils
179 containing 94.4% sand and 2.5% clay. The climate is continental with warm summers
180 and cold winters. Mean annual precipitation is 660 mm (Reich et al., 2001b).

181 The experiment was conducted on secondary successional grassland after removing the
182 previous vegetation. Starting in 1997, atmospheric CO₂ was elevated (*e*CO₂) via FACE
183 (Free air CO₂ enrichment) technology at 550 ppm in three of six rings 20 m ID. An
184 ambient CO₂ (*a*CO₂) concentration (370 ppm) was delivered to the three remaining
185 rings. Within these rings, plots of 2 × 2 m were established differing in N concentration,
186 plant species richness (not considered in the present study) and summer precipitation.
187 Nitrogen was delivered to half of the plots in May, June, and July as 4 g NH₄NO₃ m⁻²
188 yr⁻¹ slow release ammonium nitrate (ambient N = *a*N, elevated N = *e*N). This amount
189 doubles the ambient soil N availability at this site (Reich et al., 2001ab). Since 2007,
190 summer precipitation was reduced on half of the plots (*r*PREC; ambient precipitation =
191 *a*PREC) by approximately 45% with portable rain-out shelters from May to August to
192 simulate summer drought (Eisenhauer et al., 2012) as one additional future global
193 change scenario in this region (IPCC, 2007; Wuebbles and Hayhoe, 2004).

194 The main experiment was established in 1997 with plots differing in plant species
195 richness (1, 4, 9, and 16 species). Here, we focus on 48 randomly chosen 9-species plots
196 now containing 6-7 species on average and belonging to 3-4 functional groups (Reich et
197 al., 2001a; Reich et al., 2001b; Eisenhauer et al., 2012). The sown plant species
198 comprise four species of each of the functional groups C3 grasses, C4 grasses, herbs,
199 and N fixing legumes (Reich et al., 2001b). The experiment was arranged in a complete
200 factorial combination of $2 \times \text{CO}_2$ (ambient and +180 ppm), $2 \times \text{N}$ (ambient and +2 g
201 $\text{NH}_4\text{NO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), and $2 \times$ summer precipitation (ambient and -45%), replicated six
202 times each (Reich et al. 2014).

203

204 Sampling

205 In August 2010, five weeks after the last N addition campaign, three soil samples (2 cm
206 in diameter, 6 cm depth) were taken at each plot. Homogenized samples (sieving with 2
207 mm) were pooled and stored for 2 days at 4°C until extraction. Nematodes were
208 extracted from the soil samples (10 g fresh weight) by a modified Baermann method
209 (Ruess, 1995). Extraction efficiency of the Baermann method is high for sieved soil (2
210 mm) using up to 25 g fresh soil (Schulz et al., unpublished). Soil samples were placed in
211 separate plastic vessels with gauze at the bottom coated with a milk filter. The vessels
212 were put in funnels connected to glass vials and watered. Nematodes were left at 20°C
213 for 30 h to traverse the filter. Animals were killed and fixed by formaldehyde solution
214 (4 %). Nematodes were counted and a minimum of 100 individuals, if present, were
215 determined to family or genus level using 100× magnification (Zeiss, Axiovert 135) for
216 arranging them into trophic groups according to Yeates et al., (1993) and functional
217 guilds according to Ferris et al., (2001). Nematodes were identified to family level, if
218 the respective family consists of one single feeding type. If more than one feeding type

per family occurred, nematodes were identified to genus level to assign functional guilds. For instance, the family Tylenchidae consists of four different feeding types, i.e., plant ectoparasites, epidermal cell and root hair feeders, algal (or fungal), lichen or moss feeders, and hyphal-feeding nematodes. Therefore, this family had to be identified in more detail. Further, some genera cannot be assigned exclusively to one feeding guild. In these cases we decided to assign the feeding type, which is common in that family (Table 1).

Nematode community indices

To evaluate food web characteristics, Enrichment Index (EI), Structure Index (SI), and Channel Index (CI) were calculated after Ferris *et al.* (2001). These three indices are calculated independently from the weighted abundance of nematode guilds. Nematode guilds comprise bacterivores (Ba_x), fungivores (Fu_x), predators (Pr_x), and omnivores (Om_x) ranging along the *c-p* scale from $x = 1$ to $x = 5$. Nematodes of *c-p* 1 have a short life cycle, high fecundity, are tolerant to disturbance, and can be ascribed to *r*-strategists. In contrast, nematodes of *c-p* 5 produce few large eggs, have a long life cycle combined with a long generation time, and are sensitive to disturbance resembling *K*-strategists. Numbers between 1 and 5 reflect gradations between these opposing life history strategies (Neher and Darby, 2009). Plant feeders are excluded from this system as they react differently to nutrient addition (Bongers and Bongers, 1998). The relative abundance of these guilds reflects certain soil conditions and characteristics of the soil food web, such as level of enrichment, disturbance and food web complexity. The EI provides information about the resource status of the ecosystem investigated and is calculated as

$$EI = 100 \times [e/(e+b)], \quad (\text{eqn. 1})$$

with e representing the enrichment component, calculated as the weighted frequencies of Ba_1 and Fu_2 nematodes and b representing the basal food web component, calculated as the weighted frequencies of Ba_2 and Fu_2 nematodes (Ferris et al., 2001).

The Structure Index (SI) combines functional guilds of nematodes of higher $c-p$ values ranging from $c-p$ 3-5. Nematodes within these guilds represent more stable conditions, e.g., by recovering from stress and higher food web connectivity, i.e., a high degree of connectance through many interactions and, therefore, functional resilience to disturbance (Ferris et al., 2001). High SI values indicate a structured ecosystem with many trophic links, whereas low values stand for simplified and disturbed systems. It is calculated as

$$SI = 100 \times [s/(s+b)], \quad (\text{eqn. 2})$$

with s representing the structure food web component calculated as the weighted frequencies of Ba_3 - Ba_5 , Fu_3 - Fu_5 , Pr_3 - Pr_5 and Om_3 - Om_5 as well as b the basal food web component, calculated as the weighted frequencies of Ba_2 and Fu_2 .

Information about the dominant decomposition channel is provided by the Channel Index (CI), as it reflects the percentage of opportunistic fungal-feeding nematodes among the total of opportunistic fungal and bacterial-feeding nematodes. It is calculated as

$$CI = 100 \times [0.8 \times Fu_2 / (3.2 \times Ba_1 + 0.8 \times Fu_2)], \quad (\text{eqn. 3})$$

with Fu_2 representing all fungal feeders of $c-p$ 2 and Ba_1 all bacterial feeders of $c-p$ 1 and coefficients represents the population increase rate (Ferris et al., 1996). Low CI values indicate bacterial dominated decomposition whereas high values refer to a more fungal dominated system.

268

269 *Statistical analysis*

270 Three-way ANOVA (SAS 9.2, SAS Institute Inc., Cary, NC, USA) was used to test for
 271 main effects of CO₂ (ambient and elevated), N (ambient and elevated), precipitation
 272 (ambient and reduced), and all possible interactions. Nematode abundance data was log-
 273 transformed to meet the requirements of ANOVA. The effect of CO₂ was tested against
 274 the random effect of ring nested within CO₂ (Reich et al., 2001a). Following the
 275 arguments of Moran (2003), we did not correct for multiple statistical testing. Briefly,
 276 reducing alpha-error comes at the expense of increasing beta-error. Owing to the high
 277 variability and low replication often present in ecological data, ecological investigations
 278 are at risk of falsely rejecting effects that factually are true and should not further
 279 exaggerate beta-error. Nematode guilds and families comprising less than 2% of the
 280 entire population were excluded from the analysis. Treatment effects on the overall
 281 density of varying trophic groups and taxa richness are described elsewhere (Eisenhauer
 282 et al., 2012).

283

284 **Results**285 *Nematode composition*

286 Elevated CO₂ significantly decreased densities of plant feeders within *c-p* 5 nematodes
 287 (Pl₅), consisting exclusively of root-feeding Longidoridae, but the effect varied with N
 288 supply (P = 0.0117; Table A.1; Fig. 1a). At *e*CO₂, *e*N decreased Longidoridae density
 289 significantly by –65% compared to *a*N. In contrast, at *a*CO₂, *e*N significantly increased
 290 Longidoridae density by +148% compared to *a*N (Table B.1). Other plant feeders did
 291 not react significantly to the treatments although Pl₂ nematodes were always lower at

292 *r*PREC (Fig. 1b; Table A.1). Elevated N significantly increased densities of Ba₂ (P =
293 0.0112; Fig. 1c; Table A.1). Interestingly, no bacterial-feeding guild was significantly
294 influenced by CO₂ or precipitation nor by any interaction (Table A.1, Fig. 1d). Densities
295 of Fu₂ nematodes were significantly higher at *e*N (+112%) than at *a*N, but differences
296 mainly occurred at *a*CO₂ (P = 0.0454; Table A.1,B.1; Fig. 1e). In contrast, Fu₄
297 nematodes increased marginally significantly at *e*CO₂, when nitrogen was not added (P
298 = 0.0757; Fig. 1f). Omnivorous nematodes (Om₄ and Om₅) were not significantly
299 influenced by any of the treatments (Fig. 1 g,h; Table A.1), whereas Pr₄ nematodes were
300

Figure 1 The effect of CO₂ (aCO_2 = ambient CO₂, eCO_2 = elevated CO₂), N addition (aN = ambient N, eN = elevated N), and precipitation (aP = ambient precipitation, rP = reduced precipitation) on nematode functional guilds. PI = plant feeders, Ba = bacterial feeders, Fu = fungal feeders, Om = omnivores, Pr = predators. Subscript numbers refer to the related *c-p*-classification of nematodes (see text for details). Means $\pm$ SE ($n = 6$).

significantly reduced at *e*N compared to ambient N levels (-63%; $P = 0.0088$; Table A.1,B.1; Fig. 1i).

Nematode functional indices

Different components of the nematode community were influenced by the three environmental factors - most strongly by N, modestly by CO₂, and only little by precipitation. Interactions were found mainly for CO₂ × N on the level of nematode functional guilds, and for CO₂ × PREC in case of nematode indices.

The BioCON site can be classified according to the position of samples within the faunal profile based on EI and SI (Fig. 2). The different global change treatments were plotted closely, dispersing in quadrants B and C. Generally, quadrant B classifies sites being little to moderately disturbed, N enriched, with a balanced decomposition channel (i.e., bacterial vs. fungal-feeding nematodes), and a mature food web, whereas quadrant C contains undisturbed sites, moderate enrichment, decomposition channels dominated by fungi, and stable food web conditions. Here, quadrant B contained plots treated with ambient N, whereas quadrant C comprised plots with N addition, indicating a shift in decomposition channels towards fungi at *e*N. In detail, nematode communities at *e*N were significantly less structured and enriched than at *a*N, as indicated by EI ($P = 0.0014$) and SI ($P = 0.0031$; Fig. 2; Table A.1). In addition, nematode densities belonging to *c-p* 2 were significantly increased at *e*N as compared to *a*N (+46 %; $P = 0.0076$, Table A.1), whereas nematodes of the *c-p* 4 class were significantly reduced at *e*N (-36%; $P = 0.0046$; Table A.1,B.1). Moreover, nematode communities were significantly less structured (low SI) at *e*CO₂ than at *a*CO₂ ($P = 0.0419$; Table A.1). Further we found a significant effect of the interaction of PREC × CO₂ for EI and CI. *r*PREC decreased EI only at *a*CO₂, whereas EI was higher at *e*CO₂ and *r*PREC ($P =$

0.0286; Fig. 3a; Table A.1). In contrast, CI was significantly higher at *r*PREC at *a*CO₂, whereas at *e*CO₂ differences were relatively small ($P = 0.0481$; Fig. 3b; Table A.1). Further, CI was significantly higher at *e*N than at *a*N (-58% ; $P = 0.0025$; Table A.1, B.1), indicating stronger fungal contribution to decomposition processes at *e*N, whereas decomposition was mainly driven by bacteria at *a*N.

Figure 2: Enrichment Index (EI) and Structure Index (SI) trajectories for plots arranged in a full factorial combination of ambient CO₂ (*a*CO₂; triangles) or elevated CO₂ (*e*CO₂; circles), ambient N (*a*N; open symbols) or elevated N (*e*N; filled symbols), as well as ambient precipitation (*a*PREC; blue squares) and reduced precipitation (*r*PREC; red squares). Ellipses group N treatments. Continuous arrows indicate effects of *r*PREC reducing EI, whereas dotted arrows show only little effects of *a*PREC on EI ($n = 6$).

Figure 3 The effect of CO₂ (*a*CO₂ = ambient CO₂, *e*CO₂ = elevated CO₂), N (*a*N = ambient N, *e*N = elevated N), and precipitation (*a*PREC = ambient precipitation, *r*PREC = reduced precipitation) on a) Enrichment Index and b) Channel Index. Low CI values indicate bacterial dominated decomposition,

Discussion

We used nematodes as indicators of soil ecological processes as affected by elevated CO_2 , enriched N, and reduced precipitation as well as their interactions in a long-term global change experiment in grassland. Functional guilds of nematodes were significantly influenced by some of the treatments. In particular, elevated N and interactions between N and CO_2 altered the structure of nematode communities, suggesting complex changes in belowground processes in a changing world. In more detail, we found different responses of functional guilds within one trophic group indicating that interpretation on the trophic level can be misleading especially when aiming to understand changes in soil processes.

Fungal-feeding nematodes

Our hypothesis stated that $e\text{CO}_2$, $e\text{N}$, $r\text{PREC}$, and their interactions to differentially affect nematode functional guilds due to functional differences within one trophic group. In line with that hypothesis, fungal-feeding nematodes with r -strategy (Fu_2) increased on plots with N addition at $a\text{CO}_2$, whereas little differences were found at $e\text{CO}_2$. Elevated CO_2 is assumed to favor arbuscular mycorrhizal fungi (AMF) due to increased root carbon supply (Jifon et al., 2002; Treseder, 2004), whereas N fertilization reduced AMF biomass at the same site (Antoninka et al., 2011). Our results suggest that Fu_2 did not rely on AMF, because their densities increased as AMF decreased (Antoninka et al., 2011), but may feed predominantly on saprotrophic fungi. In contrast, Fu_4 followed the reverse pattern by responding negatively to N fertilization and by strongly increasing at $e\text{CO}_2$ and $a\text{N}$. This suggests that these functional guilds depend on different groups of fungi, Fu_2 on saprotrophic and Fu_4 may feed on AMF. This is in

line with Klironomos et al., (1996) suggesting a mutualistic-closed and mycorrhizal-dominated system at $e\text{CO}_2$ and a more opportunistic-open and saprobe-pathogen-dominated system at $a\text{CO}_2$ and $e\text{N}$. Our results imply that altered C and N supply to differentially affect fungal communities and thereby soil processes as saprotrophic fungi are suggested to mobilize carbon, while mycorrhizae mobilize N and P (Hobbie and Horton, 2007; Smith and Read, 2008). Changes in the importance of functional groups of fungi due to global change agents may affect carbon pools in soil, which should be tested in future research.

Bacterial-feeding nematodes

Interestingly, no bacterial-feeding guild was affected by $e\text{CO}_2$, although studies from the BioCON site reported an significantly higher labile carbon flow (Adair et al., 2011) and higher soil microbial biomass (Eisenhauer et al., 2012). Similar to our results, Hungate et al. (2000) and Yeates et al. (1997) reported no increase in bacterial-feeding nematodes despite higher microbial biomass. They argued that top-down forces, e.g., caused by increased densities of predatory microarthropods and nematodes counteracted bottom-up effects. Indeed, $e\text{CO}_2$ increased the density of gamasid mites (+143%) and Collembola (+64%) in the BioCON experiment (Eisenhauer et al., 2012), and both groups are known to feed on nematodes (Ruess et al., 2005). In addition, the abundance of ciliates increased at $e\text{CO}_2$ by +83% (Eisenhauer et al., 2012), and this may have also circumvented bottom-up effects on bacterial-feeding nematodes due to resource competition (Bergtold et al., 2005). Thus, elevated availability of labile C compounds in the soil at $e\text{CO}_2$ might have affected more competitive groups of soil biota; therefore, shifts in the composition of soil food webs likely were due to a shift in the prevalence of bottom-up vs. top-down forces. In addition, several studies exist on the effect of $e\text{CO}_2$

on nematodes showing quite diverse responses (e.g., Ayres et al., 2008; Hoeksema et al., 2000; Li et al., 2007; Niklaus et al., 2007). Yeates et al., (1999) argued that long-term responses to elevated CO₂ strongly depend on the underlying soil system and its interaction with the soil fauna, suggesting context-dependent relationships.

Elevated N availability significantly increased the density of opportunistic Ba₂ nematodes, although microbial biomass did not increase at *e*N (Eisenhauer et al., 2012). In contrast and as detailed above, microbial biomass increased at *e*CO₂ without significantly affecting any bacterial-feeding nematode guild. This may also suggests that food quality, i.e., nutrient concentrations of microorganisms, may be of greater importance for opportunistic bacterial-feeding nematodes than food quantity as reflected by microbial biomass (Schmidt et al., 2000) or microbial community composition (Chung et al., 2007). An increase in the nutrient quality of microorganisms/change in the community composition is probably induced by shifts in the quality of organic material and plant exudates delivered by plants (Bardgett and Wardle, 2010), although the quantity of rhizodeposits is reduced at *e*N (Dijkstra et al., 2005; Högberg et al., 2010).

The lack of response in Ba₁ nematodes is probably due to an increase in their densities rapidly after resource increases (Bongers and Ferris, 1999). Thus, sampling five weeks after the last experimental N addition may not reflect a prolonged increase in this group. This is in line with other studies where members of Ba₁ nematodes responded marginally to N addition (Sarathchandra et al., 2001; Wei et al., 2012). The remaining bacterial feeders of higher *c-p* classes (Ba₃ and Ba₄) decreased in numbers which supports the hypothesis that mainly opportunistic nematodes benefit from N addition and that members within one trophic group react differently due to functional differences.

Generally, it should be noted that this sampling just covered a short period in time, i.e.,

during peak biomass without covering potential temporal differences in plant and nematode communities (Viketoft et al. 2011). Future studies may also include temporal aspects allowing to better understand changes in nematode community composition due to different life strategies, e.g., by considering multiple years and/or different seasons.

Plant-feeding nematodes

Densities of root-feeding Longidoridae (*c-p* 5) decreased considerably at $e\text{CO}_2$ and $e\text{N}$ levels. Generally, $e\text{CO}_2$ enhances photosynthesis and plant growth (Ainsworth and Long, 2005; Lee et al., 2011). In the BioCON experiment, $e\text{CO}_2$ significantly increased fine root biomass (Reich et al., 2014)(+22% in 2010; P.B. Reich, unpublished data). However, Longidoridae did not benefit from enhanced fine root biomass, especially under N-rich conditions. In studies of grazed C_3 grass-dominated pasture on sand, Yeates et al. (2003) and Yeates and Newton (2009) found densities of *Longidorus elongatus* (de Man) to be significantly higher at $e\text{CO}_2$ than at $a\text{CO}_2$. This contrasts with our findings suggesting different forces in structuring the soil food web in different environmental contexts, e.g., soil type, vegetation and climate as stated above. Variable responses of plant-feeding nematodes to $e\text{CO}_2$ were reported before (Hoeksema et al., 2000; Hungate et al., 2000; Kardol et al., 2010; Neher et al., 2004; Runion et al., 1994; Wei et al., 2012; Yeates et al., 2003, 1997), indicating that effects do not solely depend on the quantity of resource inputs (when assuming a general increase in belowground inputs at $e\text{CO}_2$) (Adair et al., 2011). Moreover, the interactions between CO_2 and N argue for multifactor experiments, but also to consider different biotic (plant and animal community, SOM) and abiotic contexts (soil type, latitude) to correctly interpret different patterns. In addition, it was shown experimentally for C_3 plants that high CO_2 concentrations increased C- but also N-containing compounds like alkaloids (Ziska et

al., 2005; Matros et al., 2006), suggesting enhanced investment in plant defense (Stiling and Cornelissen, 2007; Sun et al., 2011). Thus, changes in the composition of secondary plant compounds due to elevated C and N availability may have reduced the performance of some plant feeding groups in our experiment. However, this needs further investigation as we have no data on secondary plant compounds.

The positive effect of eN at aCO_2 on Longidoridae reflect a common fertilization effect due to increased plant biomass N content in plant tissue (Reich et al., 2006b), with the latter likely representing high quality food. Other plant-feeding nematodes, such as Tylenchidae (Pl_2), were not significantly affected suggesting that those taxa are more tolerant to changes in plant physiology. In sum, changes in C and N regimes may alter plant performance and consequently have impact on trophic interactions in soil.

Predators and Omnivores

Predators and omnivores occupy positions at high trophic levels and often are used to indicate a more species-rich community and more trophic links, which is reflected by the SI (Ferris et al., 2001). SI was significantly reduced at eN indicating food web simplification compared to ambient conditions. Interestingly, only Pr_4 nematodes were significantly negatively affected by eN , whereas all omnivore groups were not significantly affected. The lack of effect on omnivores may be due to their diverse and often unknown feeding strategies hampering interpretation. Assuming similar responses to environmental changes, predators and omnivores have been combined in some studies (Li et al., 2007; Thakur et al., 2014; Zhang et al., 2012) although responses can differ strongly (Neher and Weicht, 2013). High omnivory and high link density are typical features of soil food webs (Digel et al., 2014) arguing for complex feeding

interactions, which are most likely not possible to be captured at the level of functional guilds due to multiple interactions.

Indices

Drought affected soil nematodes only slightly, providing partial support for our hypothesis that reduced precipitation would decrease sensitive nematodes while having little impact on opportunistic soil nematodes, even though summer precipitation was reduced considerably (~45%; Eisenhauer et al., 2012).

This is in accordance with other studies reporting only weak effects of soil moisture on opportunistic nematodes (Ekschmitt et al., 1999; Porazinska et al., 1998). The lack of responses of all nematode guilds to r PREC may be explained by their ability to stand dry conditions by anhydrobiosis (Treonis et al., 2000), and as the community may generally be adapted to dry conditions as it is typical for this sandy soil.

The significant effect of the interaction of $\text{CO}_2 \times \text{PREC}$ on EI was a result of a small decrease in Fu_2 and Ba_1 nematodes (numerator gets smaller) and a stronger increase in Ba_2 nematodes (denominator gets larger) at r PREC and $a\text{CO}_2$. This negative effect was not present at $e\text{CO}_2$, suggesting compensatory effects, probably as soil water content is increased due to decreased stomatal conductance at $e\text{CO}_2$ (Lee et al., 2011). Further, the CI significantly increased at a PREC and $a\text{CO}_2$, typically indicating a larger contribution of Fu_2 nematodes (Ferris et al. 2001). However, Fu_2 and Ba_1 had comparable densities at r PREC and $a\text{CO}_2$ highlighting that changes in Ba_1 , but not Fu_2 nematodes, are responsible for the significant effect on CI. This again suggests compensatory effects of $e\text{CO}_2$ and that microbial structure is more affected by water than by $e\text{CO}_2$ (Pereira et al., 2013).

Generally, effects of N fertilization on soil microbial activity are little understood (Dijkstra et al., 2005), but several studies stressed that decomposition is predominantly negatively to neutrally influenced by N fertilization (Hobbie, 2000). At our study site, N fertilization slightly increased decomposition (Knops et al., 2007). However, the decomposition channel changed as indicated by higher CI at *eN*, reflecting a stronger contribution of *Fu*₂ nematodes compared to *Ba*₁ nematodes to decomposition processes at *eN*. This may be due to a decreased C-to-N ratio of organic material being usually degraded by fungi (Ruess and Ferris, 2004; Ruess, 2003) and reduced carbon allocation to roots (Högberg et al., 2010), which are not available for *Ba*₁ nematodes. Further, as stated above, the increase in fungal decomposition at *eN* is suggested to be due to an increase in saprotrophic fungi rather than AM fungi.

Next to SI and EI, the Maturity Index (MI) often is used to describe soil health (Bongers and Bongers, 1998; Bongers, 1990). It is the result of weighted frequencies of nematode families being assigned to a specific *c-p* value, whereas SI and EI also use constants that are different for differing functional guilds. Therefore, the MI is not able to detect differences due to changes among trophic groups, but indicates overall food web simplification (Bongers and Bongers, 1998; Bongers, 1990), which was not the case in this study where functional components changed. Generally, nematode functional indices are able to integrate several nematode responses and may help to simplify processes, but based on the present results we suggest to also present data on functional guilds. Responses of functional guilds and indices were different, and interpretation of only one parameter may be misleading.

Conclusions

We showed that the responses of functional guilds within one trophic level can differ markedly. Therefore, results based on trophic levels may not reflect opposing responses within one trophic group. Although nematode identification can be challenging, we suggest that identifying nematodes and interpreting nematode data at least at the level of functional guilds will aid considerably in understanding the role of the nematode community in influencing belowground processes under global change. Further, our results show the relevance of interactive effects of CO₂, N, and precipitation on nematode communities and their functions, suggesting that long-term studies on interactive effects of global change agents are needed to improve predictions of the consequences of future global changes (Reich et al., 2014). Moreover, such experiments need to consider the intimate relationships between the aboveground and belowground subsystems and to relate changes in functional indices of soil nematodes to essential ecosystem processes, such as C dynamics.

Acknowledgements

We thank Molly Heit for help during field sampling, and Cindy Buschena, Montara Roberts, Chris Bergquist and Susan Barrott (University of Minnesota) for their help during the processing of soil samples. Simone Cesarz was funded by the Ministry of Science and Culture of Lower Saxony and the ‘Niedersächsisches Vorab’ as part of the Cluster of Excellence ‘Functional Biodiversity Research’. Nico Eisenhauer gratefully acknowledges funding by the Deutsche Forschungsgemeinschaft (DFG; Ei 862/1 and 862/2). This research has been supported by the US National Science Foundation (NSF) Long-Term Ecological Research (DEB-9411972, DEB-0080382, DEB-0620652, and

DEB-1234162), Biocomplexity Coupled Biogeochemical Cycles (DEB-0322057),
Long-Term Research in Environmental Biology (DEB-0716587, DEB-1242531) and
Ecosystem Sciences (NSF DEB-1120064) Programs; as well as the U.S. Department of
Energy Program for Ecosystem Research (DE-FG02-96ER62291) and National Institute
for Climatic Change Research (DE-FC02-06ER64158).

536

537 References

- 538 Adair, E.C., Reich, P.B., Trost, J.J., Hobbie, S.E., 2011. Elevated CO₂ stimulates
539 grassland soil respiration by increasing carbon inputs rather than by enhancing soil
540 moisture. *Glob. Chang. Biol.* 17, 3546–3563. doi:10.1111/j.1365-
541 2486.2011.02484.x
- 542 Ainsworth, E.A., Long, S.P., 2005. What have we learned from 15 years of free-air CO₂
543 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis,
544 canopy properties and plant production to rising CO₂. *New Phytol.* 165, 351–371.
545 doi:10.1111/j.1469-8137.2004.01224.x
- 546 Antoninka, A., Reich, P.B., Johnson, N.C., 2011. Seven years of carbon dioxide
547 enrichment, nitrogen fertilization and plant diversity influence arbuscular
548 mycorrhizal fungi in a grassland ecosystem. *New Phytol.* 192, 200–214.
549 doi:10.1111/j.1469-8137.2011.03776.x
- 550 Ayres, E., Wall, D., Simmons, B., Field, C., Milchunas, D., Morgan, J., Roy, J., 2008.
551 Belowground nematode herbivores are resistant to elevated atmospheric CO₂
552 concentrations in grassland ecosystems. *Soil Biol. Biochem.* 40, 978–985.
553 doi:10.1016/j.soilbio.2007.11.018
- 554 Bardgett, R.D., Wardle, D.A., 2010. Aboveground–Belowground Linkages, Biotic
555 Interactions, Ecosystem Processes, and Global Change. *Oxford Series in Ecology
556 and Evolution*, Oxford University Press, New York, USA.
- 557 Bergtold, M., Gunter, V., Traunspurger, W., 2005. Is there competition among ciliates
558 and nematodes? *Freshw. Biol.* 50, 1351–1359. doi:10.1111/j.1365-
559 2427.2005.01402.x
- 560 Bidart-Bouzat, M.G., Imeh-Nathaniel, A., 2008. Global change effects on plant
561 chemical defenses against insect herbivores. *J. Integr. Plant Biol.* 50, 1339–1354.
562 doi:10.1111/j.1744-7909.2008.00751.x

- Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. *Oecologia* 165, 553–65. doi:10.1007/s00442-011-1909-0
- Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83, 14–19.
- Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. *Appl. Soil Ecol.* 10, 239–251.
- Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. *Trends Ecol. Evol.* 14, 224–228.
- Chung, H., Zak, D.R., Reich, P.B., Ellsworth, D.S., 2007. Plant species richness, elevated CO₂, and atmospheric nitrogen deposition alter soil microbial community composition and function. *Glob. Chang. Biol.* 13, 980–989. doi:10.1111/j.1365-2486.2007.01313.x
- Clark, C.M., Tilman, D., 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* 451, 712–715. doi:10.1038/nature06503
- Digel, C., Curtsdotter, A., Riede, J., Klarner, B., Brose, U., 2014. Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. *Oikos* no–no. doi:10.1111/oik.00865
- Dijkstra, F.A., Hobbie, S.E., Reich, P.B., Knops, J.M.H., 2005. Divergent effects of elevated CO₂, N fertilization, and plant diversity on soil C and N dynamics in a grassland field experiment. *Plant Soil* 272, 41–52. doi:10.1007/s11104-004-3848-6
- Eisenhauer, N., Cesarz, S., Koller, R., Worm, K., Reich, P.B., 2012. Global change belowground: impacts of elevated CO₂, nitrogen, and summer drought on soil food webs and biodiversity. *Glob. Chang. Biol.* 18, 435–447. doi:10.1111/j.1365-2486.2011.02555.x
- Ekschmitt, K., Bakonyi, G., Bongers, M., Bongers, T., Boström, S., Anthony, G., Dogan, H., Harrison, A., Kallimanis, A., Donnell, O., Sohlenius, B., Stamou, G.P., Wolters, V., 1999. Effects of the nematofauna on microbial energy and matter transformation rates in European grassland soils. *Plant Soil* 212, 45–61.
- Ferris, H., 2010. Contribution of nematodes to the structure and function of the soil food web. *J. Nematol.* 42, 63–67.
- Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Appl. Soil Ecol.* 18, 13–29. doi:10.1016/S0929-1393(01)00152-4
- Ferris, H., Eyre, M., Venette, R.C., Lau, S.S., 1996. Population energetics of bacterial-feeding nematodes: Stage-specific development and fecundity rates. *Soil Biol. Biochem.* 28, 271–280. doi:10.1016/0038-0717(95)00127-1

- 600 Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H.,
601 Hättenschwiler, S., 2010. Diversity meets decomposition. *Trends Ecol. Evol.* 25,
602 372–380. doi:10.1016/j.tree.2010.01.010
- 603 Gross, N., Robson, T.M., Lavorel, S., Albert, C., Le Bagousse-Pinguet, Y., Guillemin,
604 R., 2008. Plant response traits mediate the effects of subalpine grasslands on soil
605 moisture. *New Phytol.* 180, 652–662. doi:10.1111/j.1469-8137.2008.02577.x
- 606 Hawkes, C. V., Kivlin, S.N., Rocca, J.D., Huguet, V., Thomsen, M.A., Suttle, K.B.,
607 2011. Fungal community responses to precipitation. *Glob. Chang. Biol.* 17, 1637–
608 1645. doi:10.1111/j.1365-2486.2010.02327.x
- 609 Hobbie, E.A., Horton, T.R., 2007. Evidence that saprotrophic fungi mobilise carbon and
610 mycorrhizal fungi mobilise nitrogen during litter decomposition. *New Phytol.* 173,
611 447–449. doi:10.1111/j.1469-8137.2007.01984.x
- 612 Hobbie, S.E., 2000. Interactions between litter lignin and soil nitrogen availability
613 during leaf litter decomposition in a hawaiian montane forest. *Ecosystems* 3, 484–
614 494. doi:10.1007/s100210000042
- 615 Hoeksema, J.D., Lussenhop, J., Teeri, J.A., 2000. Soil nematodes indicate food web
616 responses to elevated atmospheric CO₂. *Pedobiologia* 735, 725–735.
- 617 Högberg, M.N., Briones, M.J.I., Keel, S.G., Metcalfe, D.B., Campbell, C., Midwood,
618 A.J., Thornton, B., Hurry, V., Linder, S., Näsholm, T., Högberg, P., 2010.
619 Quantification of effects of season and nitrogen supply on tree below-ground
620 carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine
621 forest. *New Phytol.* 187, 485–493. doi:10.1111/j.1469-8137.2010.03274.x
- 622 Hu, S., Chapin, F.S., Firestone, M.K., Field, C.B., Chiariello, N.R., 2001. Nitrogen
623 limitation of microbial decomposition in a grassland under elevated CO₂. *Nature*
624 409, 188–191. doi:10.1038/35051576
- 625 Hungate, B.A., Jaeger III, C.H., Gamara, G., Chapin III, F.S., Field, C.B., 2000. Soil
626 microbiota in two annual grasslands: responses to elevated atmospheric CO₂.
627 *Oecologia* 124, 589–598. doi:10.1007/s004420000405
- 628 IPCC, 2007. *Climate Change 2007: The Physical Science Basis. Contribution of*
629 *Working Group I to the Fourth Assessment Report of the Intergovernmental Panel*
630 *on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and
631 New York, NY, USA.
- 632 Jifon, J.L., Graham, J.H., Drouillard, D.L., Syvertsen, J.P., 2002. Growth depression of
633 mycorrhizal Citrus seedlings grown at high phosphorus supply is mitigated by
634 elevated CO₂. *New Phytol.* 153, 133–142. doi:10.1046/j.0028-646X.2001.00294.x
- 635 Kardol, P., Cregger, M.A., Company, C.E., Classen, A.T., 2010. Soil ecosystem
636 functioning under climate change: plant species and community effects. *Ecology*
637 91, 767–781.

- 638 Keeler, B.L., Hobbie, S.E., Kellogg, L.E., 2008. Effects of long-term nitrogen addition
639 on microbial enzyme activity in eight forested and grassland sites: implications for
640 litter and soil organic matter decomposition. *Ecosystems* 12, 1–15.
641 doi:10.1007/s10021-008-9199-z
- 642 Kerr, R.A., 2007. Global warming is changing the world. *Science* 316, 188–190.
- 643 Klarner, B., Maraun, M., Scheu, S., 2013. Trophic diversity and niche partitioning in a
644 species rich predator guild - Natural variations in stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$,
645 $^{15}\text{N}/^{14}\text{N}$) of mesostigmatid mites (Acari, Mesostigmata) from Central European
646 beech forests. *Soil Biol. Biochem.* 57, 327–333.
- 647 Klironomos, J.N., Rillig, M.C., Allen, M.F., 1996. Below-ground microbial and
648 microfaunal responses to *Artemisia tridentata* grown under elevated atmospheric.
649 *Funct. Ecol.* 10, 527–534.
- 650 Knops, J.M.H., Naeem, S., Reich, P.B., 2007. The impact of elevated CO_2 , increased
651 nitrogen availability and biodiversity on plant tissue quality and decomposition.
652 *Glob. Chang. Biol.* 13, 1960–1971. doi:10.1111/j.1365-2486.2007.01405.x
- 653 Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a
654 meta-analysis. *Ecology* 86, 3252–3257.
- 655 Körner, C., 2000. Biosphere responses to CO_2 enrichment. *Ecol. Appl.* 10, 1590–1619.
- 656 Kuzyakov, Y., Gavrichkova, O., 2010. REVIEW: Time lag between photosynthesis and
657 carbon dioxide efflux from soil: a review of mechanisms and controls. *Glob.*
658 *Chang. Biol.* 16, 3386–3406. doi:10.1111/j.1365-2486.2010.02179.x
- 659 Lau, J.A., Tiffin, P., 2009. Elevated carbon dioxide concentrations indirectly affect
660 plant fitness by altering plant tolerance to herbivory. *Oecologia* 161, 401–410.
661 doi:10.1007/s00442-009-1384-z
- 662 LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in
663 terrestrial ecosystems is globally distributed. *Ecol. Lett.* 89, 371–379.
- 664 Lee, T.D., Barrott, S.H., Reich, P.B., 2011. Photosynthetic responses of 13 grassland
665 species across 11 years of free-air CO_2 enrichment is modest, consistent and
666 independent of N supply. *Glob. Chang. Biol.* 17, 2893–2904. doi:10.1111/j.1365-
667 2486.2011.02435.x
- 668 Li, Q., Liang, W., Jiang, Y., Shi, Y., Zhu, J., Neher, D.A., 2007. Effect of elevated CO_2
669 and N fertilisation on soil nematode abundance and diversity in a wheat field.
670 *Appl. Soil Ecol.* 36, 63–69. doi:10.1016/j.apsoil.2006.11.003
- 671 Lindberg, N., Engtsson, J.B., Persson, T., 2002. Effects of experimental irrigation and
672 drought on the composition and diversity of soil fauna in a coniferous stand. *J.*
673 *Appl. Ecol.* 39, 924–936. doi:10.1046/j.1365-2664.2002.00769.x
- 674 Matros, A., Amme, S., Kettig, B., Buck-Sorlin, G.H., Sonnewald, U., Mock, H.-P.,
675 2006. Growth at elevated CO_2 concentrations leads to modified profiles of

- secondary metabolites in tobacco cv. SamsunNN and to increased resistance against infection with potato virus Y. *Plant, Cell Environ.* 29, 126–137.
- Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological. *OIKOS* 100, 403–405.
- Neher, D.A., Darby, B.J., 2009. Community indices, in: Wilson, M.J., Kakouli-Duarte, T. (Eds.), *Nematodes as Environmental Indicators*. CABI, Wallingford, UK, pp. 107–123.
- Neher, D.A., Weicht, T.R., 2013. Nematode Genera in Forest Soil Respond Differentially to Elevated CO₂. *J. Nematol.* 45, 214–222.
- Neher, D.A., Weicht, T.R., Moorhead, D.L., Sinsabaugh, R.L., 2004. Elevated CO₂ alters functional attributes of nematode communities in forest soils. *Funct. Ecol.* 18, 584–591. doi:10.1111/j.0269-8463.2004.00866.x
- Niklaus, P. a, Alphei, J., Kampichler, C., Kandeler, E., Körner, C., Tscherko, D., Wohlfender, M., 2007. Interactive effects of plant species diversity and elevated CO₂ on soil biota and nutrient cycling. *Ecology* 88, 3153–63.
- Okada, H., Harada, H., 2007. Effects of tillage and fertilizer on nematode communities in a Japanese soybean field. *Appl. Soil Ecol.* 35, 582–598. doi:10.1016/j.apsoil.2006.09.008
- Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C., Fasth, B., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* 315, 361–364.
- Pereira, E.I.P., Chung, H., Scow, K., Six, J., 2013. Microbial communities and soil structure are affected by reduced precipitation, but not by elevated carbon dioxide. *Soil Sci. Soc. Am. J.* 77, 482–488.
- Porazinska, L., McSorley, R., Duncan, L.W., Gallaher, R.N., Wheaton, T.A., Parsons, L.R., 1998. Relationships between soil chemical status, soil nematode community, and sustainability indices. *Nematropica* 28, 249–262.
- Reich, P.B., 2009. Elevated CO₂ reduces losses of plant diversity caused by nitrogen deposition. *Science* 326, 1399–1402. doi:10.1126/science.1178820
- Reich, P.B., Hobbie, S.E., Lee, T., Ellsworth, D.S., West, J.B., Tilman, D., Knops, J.M.H., Naeem, S., Trost, J., 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* 440, 922–925. doi:10.1038/nature04486
- Reich, P.B., Hobbie, S.E., Lee, T.D., 2014. Plant growth enhancement by elevated CO₂ eliminated by joint water and nitrogen limitation. *Nat. Geosci.* 1–5. doi:10.1038/ngeo2284

- Reich, P.B., Hungate, B.A., Luo, Y., 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annu. Rev. Ecol. Evol. Syst.* 37, 611–636. doi:10.1146/annurev.ecolsys.37.091305.110039
- Reich, P.B., Knops, J., Tilman, D., Craine, J., Ellsworth, D.S., Tjoelker, M., Lee, T., Wedin, D., Naeem, S., Bahaeddin, D., Hendrey, G., Jose, S., Wrage, K., Goth, J., Bengston, W., 2001a. Plant diversity enhances ecosystem responses to elevated CO₂ and nitrogen deposition. *Nature* 411, 809–812. doi:10.1038/35081122
- Reich, P.B., Peterson, D.W., Wedin, D.A., Wrage, K., 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest. *Ecology* 82, 1703–1719.
- Reich, P.B., Tilman, D., Craine, J., Ellsworth, D.S., Tjoelker, M.G., Knops, J., Wedin, D., Naeem, S., Bahaeddin, D., Goth, J., Bengston, W., Lee, T.D., 2001b. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytol.* 150, 435–448. doi:10.1046/j.1469-8137.2001.00114.x
- Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336, 589–592. doi:10.1126/science.1217909
- Rogelj, J., Meinshausen, M., Knutti, R., 2012. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. *Nat. Clim. Chang.* 2, 248–253. doi:10.1038/nclimate1385
- Ruess, L., 1995. Studies on the nematode fauna of an acid forest soil: spatial disturbance and extraction. *Nematologica* 41, 229–239.
- Ruess, L., 2003. Nematode soil faunal analysis of decomposition pathways in different ecosystems. *Nematology* 5, 179–181.
- Ruess, L., Ferris, H., 2004. Decomposition pathways and successional changes. *Nematol. Monogr. Perspect.* 2, 547–556.
- Ruess, L., Tiunov, A., Haubert, D., Richnow, H.H., Häggblom, M.M., Scheu, S., 2005. Carbon stable isotope fractionation and trophic transfer of fatty acids in fungal based soil food chains. *Soil Biol. Biochem.* 37, 945–953. doi:10.1016/j.soilbio.2004.09.015
- Runion, G.B., Curl, E.A., Rogers, H.H., Backman, P.A., 1994. Effects of free-air CO₂ enrichment on microbial populations in the rhizosphere and phyllosphere of cotton. *Agric. For. Meteorol.* 70, 117–130.
- Sarathchandra, S.U., Ghani, A., Yeates, G.W., Burch, G., Cox, N.R., 2001. Effect of nitrogen and phosphate fertilisers on microbial and nematode diversity in pasture soils. *Soil Biol. Biochem.* 33, 953–964. doi:10.1016/S0038-0717(00)00245-5
- Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48, 7–20.

- Schmidt, I.K., Ruess, L., Bååth, E., Ekelund, F., Jonasson, S., 2000. Long-term manipulation of the microbes and microfauna of two subarctic heaths by addition of fungicide, bactericide, carbon and fertilizer. *Soil Biol. Biochem.* 32, 707–720.
- Schulze, E.D., Freibauer, A., 2005. Carbon unlocked from soils. *Nature* 437, 11–12.
- Smith, S., Read, D.J., 2008. *Mycorrhizal symbiosis*. Cambridge, UK, Academic Press.
- Stiling, P., Cornelissen, T., 2007. How does elevated carbon dioxide (CO₂) affect plant–herbivore interactions? A field experiment and meta-analysis of CO₂-mediated changes on plant chemistry and herbivore performance. *Glob. Chang. Biol.* 13, 1823–1842. doi:10.1111/j.1365-2486.2007.01392.x
- Sun, Y., Yin, J., Cao, H., Li, C., Kang, L., Ge, F., 2011. Elevated CO₂ influences nematode-induced defense responses of tomato genotypes differing in the JA pathway. *PLoS One* 6, e19751. doi:10.1371/journal.pone.0019751
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley.
- Thakur, M.P., Reich, P.B., Fisichelli, N.A., Stefanski, A., Cesarz, S., Dobies, T., Rich, R.L., Hobbie, S.E., Eisenhauer, N., 2014. Nematode community shifts in response to experimental warming and canopy conditions are associated with plant community changes in the temperate-boreal forest ecotone. *Oecologia* 175, 713–723. doi:10.1007/s00442-014-2927-5
- Treonis, A.M., Wall, D.H., Virginia, R.A., 2000. The use of anhydrobiosis by soil nematodes in the Antarctic Dry Valleys. *Funct. Ecol.* 14, 460–467. doi:10.1046/j.1365-2435.2000.00442.x
- Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytol.* 164, 347–355. doi:10.1111/j.1469-8137.2004.01159.x
- Wardle, D.A., Verhoef, H.A., Clarholm, M., 1998. Trophic relationships in the soil microfood-web: predicting the responses to a changing global. *Glob. Chang. Biol.* 4, 713–727.
- Wei, C., Zheng, H., Li, Q., Lü, X., Yu, Q., Zhang, H., Chen, Q., He, N., Kardol, P., Liang, W., Han, X., 2012. Nitrogen Addition Regulates Soil Nematode Community Composition through Ammonium Suppression. *PLoS One* 7, e43384. doi:10.1371/journal.pone.0043384
- Wuebbles, D.J., Hayhoe, K., 2004. Climate change projections for the United States Midwest. *Mitig. Adapt. Strateg. Glob. Chang.* 9, 335–363.
- Yeates, G.W., 2010. Nematodes in Ecological Webs, in: *Encyclopedia of Life Science*. John Wiley & Sons, Ltd: Chichester, pp. 1–11. doi:10.1002/9780470015902.a0021913

- 788 Yeates, G.W., Bongers, T., de Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993.
789 Feeding habits in soil nematode families and genera - an outline for soil ecologist.
790 J. Nematol. 25, 315–331.
- 791 Yeates, G.W., Newton, P.C.D., Ross, D.J., 1999. Response of soil nematode fauna to
792 naturally elevated CO₂ levels influenced by soil pattern. Nematology 1, 285–293.
- 793 Yeates, G.W., Newton, P.C.D., Ross, D.J., 2003. Significant changes in soil microfauna
794 in grazed pasture under elevated carbon dioxide. Biol. Fertil. Soils 38, 319–326.
795 doi:10.1007/s00374-003-0659-5
- 796 Yeates, G.W., Tate, K.R., Newton, P.C.D., 1997. Response of the fauna of a grassland
797 soil to doubling of atmospheric carbon dioxide concentration. Biol. Fertil. Soils 25,
798 307–315. doi:10.1007/s003740050320
- 799 Zhang, R., Wienhold, B.J., 2002. The effect of soil moisture on mineral nitrogen , soil
800 electrical conductivity , and pH. Nutr. Cycl. Agroecosystems 63, 251–254.
- 801 Zhang, X., Li, Q., Zhu, A., Liang, W., Zhang, J., Steinberger, Y., 2012. Effects of
802 tillage and residue management on soil nematode communities in North China.
803 Ecol. Indic. 13, 75–81. doi:10.1016/j.ecolind.2011.05.009
- 804 Ziska, L.H., Emche, S.D., Johnson, E.L., George, K., Reed, D.R., Sicher, R.C., 2005.
805 Alterations in the production and concentration of selected alkaloids as a function
806 of rising atmospheric carbon dioxide and air temperature: implications for ethno-
807 pharmacology. Glob. Chang. Biol. 11, 1789–1807.
- 808

Table 1: List of nematode taxa identified. If more than one feeding type occurred within one family, taxa were identified to the genus level to assign functional guilds after Ferris et al. (2001). If one feeding type is suggested to occur more than once in one genus, the prevailing feeding type was chosen. Asterisks indicate different feeding types within one taxon. Families are given in bold. Taxa are sorted according to trophic group and their c-p values according to Bongers (1990): 1d: plant ectoparasites, 1e: epidermal cell and root hair feeders, 1f: algal (or fungal), lichen or moss feeders, 2: hyphal-feeding, 3: bacterial-feeding, 5: animal predation, 5a: predators (ingesters), 8: omnivorous (after Yeates et al. (1993)).

Trophic group	c-p value	Family and respective genera identified when different feeding types co-occur in one family	Feeding types in family/genera	Assigned functional guild
Plant feeders	2	Tylenchidae*	1d, 1e, 1f, 2	PI2
	2	<i>Filenchus</i>	1e	PI2
	2	<i>Lelenchus</i>	1e	PI2
	2	<i>Malenchus</i>	1e	PI2
	2	<i>Aglenchus</i>	1e	PI2
	2	<i>Coslenchus</i>	1e	PI2
	2	Tylodoridae	1d	PI2
	3	Criconematidae	1d	PI3
Bacterial feeders	5	Longidoridae	1d	PI5
	1	Bunonematidae	3	Ba1
	1	Monhysteridae	3	Ba1
	1	Rhabditidae	3	Ba1
	2	Cephalobidae	3	Ba2
	2	Plectidae	3	Ba2
	3	Diplopeltidae	3	Ba3
	3	Odontolaimidae	3	Ba3
	3	Prismatolaimidae	3	Ba3
	3	Teratocephalidae	3	Ba3
Fungal feeders	4	Alaimidae	3	Ba4
	2	Aphelenchidae*	1e, 2	Fu2
	2	<i>Aphelenchus*</i>	1e, 2	Fu2
	2	<i>Paraphelenchus</i>	2	Fu2
	2	Aphelenchoididae*	1b, 1e, 1f, 2, 5b	Fu2
	2	<i>Aphelenchoides*</i>	1b, 1e, 1f, 2	Fu2
	2	<i>Aprutides</i>	2	Fu2
	2	<i>Pseudhalenchus</i>	2	Fu2
	4	Leptonchidae*	2, 8	Fu4
	4	<i>Doryllium</i>	2	Fu4
	4	<i>Funaria</i>	2	Fu4
	4	<i>Leptonchus</i>	2	Fu4
	4	<i>Tylencholaimus</i>	2	Fu4
Omnivores	4	<i>Dorylaimoides</i>	8	Om4
	4	Qudsianematidae*	5, 8	Om4
	4	<i>Dorydorella</i>	8	Om4
	4	<i>Kochinema</i>	8	Om4
	4	<i>Thonus*</i>	5, 8	Om4
	4	<i>Labronema*</i>	5, 8	Om4
	4	<i>Eudorylaimus</i>	5, 8	Om4
	5	Aporcelaimidae	5, 8	Om5
	5	<i>Aporcelaimium</i>	8	Om5
	5	<i>Aporcelaimus</i>	5, 8	Om5
	5	<i>Torumanawa</i>	8	Om5
	5	<i>Aporcelaimellus</i>	5, 8	Om5
	5	Thornenematidae	8	Om5
Predators	4	Mononchidae	5a	Pr4

5 **Discolaimidae**

5

Pr5

Table A.1 ANOVA table of *F*- and *P*-values on the effects of CO₂ (ambient and elevated), N (ambient and elevated), summer precipitation (PREC: ambient and reduced precipitation), and all possible interactions for a) the colonizer–persister (*c-p*) scale after Bongers (1990), on b) functional guilds after Ferris et al., (2001), and c) faunal profile indices after Ferris et al. (2001) and the MI after Bongers (1990). Pl = plant feeders, Ba = bacterial feeders, Fu = fungal feeders, Om = omnivores, Pr = predators, subscript numbers indicate the corresponding *c-p* classification, EI = Enrichment Index, SI = Structure Index, CI = Channel Index, MI = Maturity Index. Arrows indicate the direction of treatment effects. ↑ = increase in abundance at elevated CO₂ and elevated N or at reduced level of precipitation, ↓ = decrease. Rare groups are not displayed and were not analyzed with ANOVA due to very low densities (< 2%). The *c-p* scale does not consider plant-feeding nematodes as they react differently to nutrient addition (Bongers and Bongers, 1998). For means see Table B.1.

	CO ₂		N		PREC		CO ₂ × N		CO ₂ × PREC		N × PREC		CO ₂ × N × PREC			
	F	P	F	P	F	P	F	P	F	P	F	P	F	P		
a) c-p-classes																
c-p 1	3.72	0.0617	1.58	0.2162	0.10	0.7591	0.23	0.6316	3.09	0.0873	0.06	0.8079	0.05	0.8278		
c-p 2	0.01	0.9342	8.01	0.0076	↑	0.15	0.6972	1.78	0.1911	0.07	0.7996	0.88	0.3544	1.61	0.2125	
c-p 3	0.07	0.7944	0.06	0.8034	2.53	0.1204	0.01	0.9143	0.41	0.5256	0.03	0.8616	3.70	0.0623		
c-p 4	0.92	0.3447	9.16	0.0046	↓	1.74	0.1949	3.17	0.0835	0.10	0.7590	2.28	0.1399	0.96	0.3346	
c-p 5	0.58	0.4517	0.14	0.7112	0.22	0.6404	1.54	0.2222	0.18	0.6746	0.62	0.4358	0.09	0.7712		
b) Functional guilds																
Pl ₂	0.00	0.9939	0.01	0.9386	1.83	0.1851	0.50	0.4861	0.02	0.8951	0.06	0.8003	0.00	0.9603		
Pl ₅	4.89	0.0922	0.88	0.3544	0.05	0.8203	7.06	0.0117	0.00	0.9563	0.25	0.6210	0.12	0.7295		
Ba ₁	1.47	0.2930	1.58	0.2162	0.10	0.7591	0.23	0.6316	3.09	0.0873	0.06	0.8079	0.05	0.8278		
Ba ₂	0.06	0.8118	7.16	0.0112	↑	1.36	0.2506	0.33	0.5669	0.12	0.7331	0.51	0.4786	2.93	0.0956	
Ba ₃	0.09	0.7804	0.06	0.8034	2.53	0.1204	0.01	0.9143	0.41	0.5256	0.03	0.8616	3.70	0.0623		
Fu ₂	0.49	0.5230	5.35	0.0266	↑	1.73	0.1964	4.30	0.0454	0.00	0.9870	0.81	0.3745	0.05	0.8280	
Fu ₄	0.55	0.4995	2.23	0.1437	2.75	0.1059	3.35	0.0757	0.06	0.8007	0.06	0.8091	1.94	0.1721		
Om ₄	1.24	0.3292	2.44	0.1267	1.60	0.2145	2.14	0.1517	0.08	0.7744	2.23	0.1437	0.14	0.7118		
Om ₅	0.19	0.6842	0.24	0.6291	0.46	0.5035	1.48	0.2312	0.09	0.7696	0.48	0.4914	0.13	0.7240		
Pr ₄	1.16	0.3444	7.68	0.0088	↓	0.09	0.7677	0.16	0.6931	0.16	0.6894	1.94	0.1717	0.11	0.7404	
c) Indices																
EI	6.42	0.0688	11.97	0.0014	↓	1.38	0.2480	0.17	0.6812	5.20	0.0286	0.59	0.4492	0.38	0.5429	
SI	10.67	0.0419	↓	10.09	0.0031	↓	0.00	0.9813	0.02	0.9030	0.12	0.7325	0.85	0.3638	0.92	0.3439
CI	1.84	0.2470	10.59	0.0025	↑	0.56	0.4572	2.25	0.1423	4.19	0.0481	2.94	0.0950	0.83	0.3682	
MI	4.45	0.1064	2.50	0.1228	0.29	0.5915	0.33	0.5685	0.62	0.4346	0.43	0.5173	0.07	0.7862		

Table B.1 Mean $\pm$ SE of abundance (Individuals g^{-1} soil dry weight) for a) *c-p* scale, b) functional guilds, and c) Enrichment Index (EI), Structure Index (SI), and Channel Index (CI) as affected by of CO_2 (ambient = $a\text{CO}_2$, elevated = $e\text{CO}_2$), nitrogen (ambient = $a\text{N}$, elevated = $e\text{N}$), and precipitation (ambient = $a\text{PREC}$, elevated = $r\text{PREC}$). Pl = plant feeders, Ba = bacterial feeders, Fu = fungal feeders, Om = omnivores, Pr = predators, subscript numbers indicate the corresponding *c-p* classification. The *c-p* scale does not consider plant-feeding nematodes as they react differently to nutrient addition (Bongers and Bongers, 1998). * = not analyzed with ANOVA due to very low densities ($< 2\%$).

	$a\text{CO}_2$				$e\text{CO}_2$			
	$a\text{N}$		$e\text{N}$		$a\text{N}$		$e\text{N}$	
	$a\text{PREC}$	$r\text{PREC}$	$a\text{PREC}$	$r\text{PREC}$	$a\text{PREC}$	$r\text{PREC}$	$a\text{PREC}$	$r\text{PREC}$
a) <i>c-p</i> classes								
<i>c-p</i> 1	2.81 $\pm$ 0.75	1.89 $\pm$ 0.69	2.41 $\pm$ 0.48	2.07 $\pm$ 1.38	3.06 $\pm$ 0.63	4.54 $\pm$ 1.00	3.09 $\pm$ 1.61	3.51 $\pm$ 1.29
<i>c-p</i> 2	5.79 $\pm$ 1.11	4.72 $\pm$ 0.89	8.29 $\pm$ 1.64	11.59 $\pm$ 2.27	6.35 $\pm$ 1.41	6.83 $\pm$ 1.33	9.03 $\pm$ 2.92	8.41 $\pm$ 1.81
<i>c-p</i> 3	2.93 $\pm$ 0.74	0.90 $\pm$ 0.37	1.84 $\pm$ 0.61	1.54 $\pm$ 0.37	2.07 $\pm$ 1.23	1.82 $\pm$ 0.47	2.12 $\pm$ 0.60	1.18 $\pm$ 0.62
<i>c-p</i> 4	3.33 $\pm$ 0.69	2.93 $\pm$ 0.42	1.89 $\pm$ 0.34	3.79 $\pm$ 0.84	3.77 $\pm$ 0.89	4.99 $\pm$ 1.87	1.34 $\pm$ 0.28	2.50 $\pm$ 1.04
<i>c-p</i> 5	1.50 $\pm$ 0.31	1.27 $\pm$ 0.26	1.16 $\pm$ 0.33	1.40 $\pm$ 0.41	0.90 $\pm$ 0.15	1.01 $\pm$ 0.27	1.38 $\pm$ 0.54	1.55 $\pm$ 0.45
b) Functional guilds								
Pl ₂	2.06 $\pm$ 1.48	1.25 $\pm$ 0.70	1.48 $\pm$ 0.49	0.64 $\pm$ 0.21	1.39 $\pm$ 0.69	0.71 $\pm$ 0.30	2.08 $\pm$ 1.26	0.87 $\pm$ 0.31
Pl ₃ *	0.00 $\pm$ 0.00	0.09 $\pm$ 0.09	0.11 $\pm$ 0.08	0.03 $\pm$ 0.03	0.00 $\pm$ 0.00	0.09 $\pm$ 0.06	0.00 $\pm$ 0.00	0.26 $\pm$ 0.13
Pl ₅	1.13 $\pm$ 0.72	1.25 $\pm$ 0.74	3.20 $\pm$ 1.29	2.72 $\pm$ 0.82	0.70 $\pm$ 0.29	0.50 $\pm$ 0.22	0.11 $\pm$ 0.08	0.31 $\pm$ 0.17
Ba ₁	2.81 $\pm$ 0.75	1.89 $\pm$ 0.69	2.41 $\pm$ 0.48	2.07 $\pm$ 1.38	3.06 $\pm$ 0.63	4.54 $\pm$ 1.00	3.09 $\pm$ 1.61	3.51 $\pm$ 1.29
Ba ₂	4.52 $\pm$ 0.83	4.06 $\pm$ 0.78	5.18 $\pm$ 0.81	8.44 $\pm$ 1.02	4.76 $\pm$ 1.44	5.92 $\pm$ 1.27	7.31 $\pm$ 2.10	7.00 $\pm$ 1.48
Ba ₃	2.93 $\pm$ 0.74	0.90 $\pm$ 0.37	1.84 $\pm$ 0.61	1.54 $\pm$ 0.37	2.07 $\pm$ 1.23	1.82 $\pm$ 0.47	2.12 $\pm$ 0.60	1.18 $\pm$ 0.62
Ba ₄ *	0.02 $\pm$ 0.02	0.02 $\pm$ 0.02	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.10 $\pm$ 0.07	0.06 $\pm$ 0.06	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
Fu ₂	1.27 $\pm$ 0.42	0.65 $\pm$ 0.29	3.11 $\pm$ 0.92	3.15 $\pm$ 1.43	1.60 $\pm$ 0.41	0.91 $\pm$ 0.18	1.72 $\pm$ 0.85	1.42 $\pm$ 0.51
Fu ₄	0.13 $\pm$ 0.13	0.39 $\pm$ 0.27	0.43 $\pm$ 0.28	0.77 $\pm$ 0.49	0.90 $\pm$ 0.36	2.53 $\pm$ 1.20	0.58 $\pm$ 0.29	0.70 $\pm$ 0.40
Om ₄	1.93 $\pm$ 0.60	1.72 $\pm$ 0.35	1.24 $\pm$ 0.23	2.55 $\pm$ 0.65	2.07 $\pm$ 0.64	2.02 $\pm$ 0.74	0.61 $\pm$ 0.22	1.49 $\pm$ 0.72
Om ₅	1.37 $\pm$ 0.23	1.23 $\pm$ 0.23	1.10 $\pm$ 0.34	1.40 $\pm$ 0.41	0.86 $\pm$ 0.15	1.01 $\pm$ 0.27	1.38 $\pm$ 0.54	1.50 $\pm$ 0.41
Pr ₄	1.25 $\pm$ 0.58	0.80 $\pm$ 0.34	0.21 $\pm$ 0.18	0.47 $\pm$ 0.25	0.70 $\pm$ 0.15	0.38 $\pm$ 0.16	0.15 $\pm$ 0.07	0.31 $\pm$ 0.18
Pr ₅ *	0.13 $\pm$ 0.13	0.03 $\pm$ 0.03	0.07 $\pm$ 0.07	0.00 $\pm$ 0.00	0.04 $\pm$ 0.04	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.05 $\pm$ 0.05
c) Indices								
EI	57.21 $\pm$ 5.88	49.59 $\pm$ 5.32	52.12 $\pm$ 4.58	30.96 $\pm$ 7.15	61.30 $\pm$ 4.50	66.54 $\pm$ 2.83	45.62 $\pm$ 7.95	49.59 $\pm$ 6.39
SI	85.25 $\pm$ 2.68	83.69 $\pm$ 3.43	72.07 $\pm$ 4.31	70.82 $\pm$ 5.00	81.36 $\pm$ 4.02	75.34 $\pm$ 6.68	62.34 $\pm$ 7.96	70.81 $\pm$ 5.25
CI	7.87 $\pm$ 2.91	10.02 $\pm$ 4.25	18.24 $\pm$ 2.76	34.29 $\pm$ 9.93	10.91 $\pm$ 3.80	4.06 $\pm$ 0.91	14.04 $\pm$ 5.33	12.47 $\pm$ 4.55

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Global change and soil nematode communities

Figure 1

Figure 2

Figure 3