The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons

Julia Siebert[1,2,§,], Marie Sünnemann[1,3,§], Harald Auge[1,4], Sigrid Berger[4], Simone Cesarz[1,2], Marcel Ciobanu[5], Nico Eisenhauer[1,2]*

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

2 Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany

3 Martin-Luther-University Halle-Wittenberg, Leibniz Institute of Plant Biochemistry, Weinberg 3, 06120 Halle (Saale), Germany

4 Department of Community Ecology, Helmholtz-Centre for Environmental Research – UFZ, Theodor-Lieser-Str. 4, 06120 Halle, Germany

5 Institute of Biological Research, Branch of the National Institute of Research and Development for Biological Sciences, 48 Republicii Street, 400015 Cluj-Napoca, Romania

[§] these authors contributed equally to this work

**corresponding author (julia.siebert@idiv.de)*

Abstract

Anthropogenic global change alters the activity and functional composition of soil communities that are responsible for crucial ecosystem functions and services. Two of the most pervasive global change drivers are drought and nutrient enrichment. However, the responses of soil organisms to interacting global change drivers remain widely unknown. We tested the interactive effects of extreme drought and fertilization on soil biota ranging from microbes to invertebrates across all seasons. We expected drought to reduce the activity of soil organisms and nutrient addition to induce positive bottom-up effects via increased plant productivity. Furthermore, we hypothesized fertilization to reinforce drought effects through enhanced plant growth, resulting in aggravated soil conditions. Our results revealed that drought had detrimental effects on soil invertebrate feeding activity and simplified nematode community structure, whereas soil microbial activity and biomass were unaffected. Microbial biomass increased in response to nutrient addition, whereas invertebrate feeding activity substantially declined. Notably, these effects were consistent across seasons. The dissimilar responses suggest that soil biota differ vastly in their vulnerability to global change drivers. As decomposition and nutrient cycling are driven by the interdependent concurrence of microbial and faunal activity, this may imply far-reaching consequences for crucial ecosystem processes in a changing world.

38 # Introduction

39 Anthropogenic global environmental change affects ecosystem properties worldwide and threatens
40 important ecosystem functions (Vitousek, 1994; Steffen *et al.*, 2006). Climate change is predicted to alter
41 precipitation regimes towards more frequent and severe drought events in the future (IPCC, 2007).
42 Simultaneously, human activities, such as fossil fuel combustion and fertilization, are causing an
43 acceleration of the turnover rates of the nitrogen cycle and will double N-deposition in the future
44 (Lamarque *et al.*, 2005; Galloway *et al.*, 2008). The same is true for phosphorous inputs, which also
45 increased at a global scale (Wang *et al.*, 2015a). Thus, multiple global change drivers are occurring side by
46 side, and their effects are not necessarily additive or antagonistic. Our knowledge on their interactive
47 effects, however, is still highly limited (De Vries *et al.*, 2012; Eisenhauer *et al.*, 2012). This is particularly
48 true for the responses of soil organisms, which mediate crucial ecosystem functions and services, such as
49 nutrient cycling and decomposition (Oliver and Gregory, 2015; Wall *et al.*, 2015). Their significant role is
50 not adequately reflected in the body of global change literature yet. However, a comprehensive
51 understanding of above- and belowground dynamics is key to predict the responses of terrestrial
52 ecosystems in a changing world (Eisenhauer *et al.*, 2012).

53

54 Many soil organisms are dependent on a water-saturated atmosphere or on water films on soil aggregates
55 (Orchard and Cook, 1983; Baldrian *et al.*, 2010; Blankinship *et al.*, 2011; Riutta *et al.*, 2016). Altered
56 precipitation patterns will result in drought periods, which are likely to have substantial effects on their
57 abundances and community structure, thus affecting important soil organism-mediated ecosystem
58 processes. Previous studies reported detrimental effects of drought on soil microbial respiration and
59 biomass as well as a reduction of the diversity of microbial communities (Hueso *et al.*, 2012). Furthermore,
60 drought was shown to cause a decline in soil microarthropod abundances (Lindberg *et al.*, 2002). In

contrast, drought seems to have only marginal effects on nematode community composition (Cesarz *et al.*, 2015). Yet, a reduction of soil moisture content can induce community shifts *via* lower trophic levels, often favoring fungal-feeding nematodes over bacteria-feeders, as fungi perform relatively better under dry conditions (Kardol *et al.*, 2010; Cesarz *et al.*, 2015).

Nutrient enrichment is another key factor that affects the soil community by altering the physical and chemical properties of the soil, e.g., by influencing pH-value, soil porosity, and organic fractions (Marinari *et al.*, 2000; Galantini and Rosell, 2006; Liu *et al.*, 2010). Nitrogen addition has been identified to decrease soil microbial respiration and biomass, often leading to shifts in the soil microbial community composition under the use of mineral fertilizer (NPK) (Treseder, 2008; Ramirez *et al.*, 2010; Pan *et al.*, 2014). On the other hand, fertilization treatments were shown to increase soil microbial catabolic and functional diversity (Dan *et al.*, 2008; Li *et al.*, 2014). Furthermore, nitrogen addition alters the nematode community structure towards bacterivores, thus promoting the bacterial-dominated decomposition pathway (Song *et al.*, 2016), and was shown to simply communities (Cesarz *et al.*, 2015). At the same time, nitrogen enrichment is one of the major drivers determining aboveground primary production (Stevens *et al.*, 2015). Nitrogen and phosphorous addition are known to increase total aboveground biomass and consequently the quantity and quality of plant litter input to the soil (Liu and Greaver, 2010; Li *et al.*, 2014). This enhances resource availability via bottom-up effects and can therefore increase soil microarthropod abundances (Sjursen *et al.*, 2005). Concurrently, the fertilization-induced increase in aboveground biomass may cause higher transpiration rates, which are likely to reinforce drought effects on soil organisms (Craven *et al.*, 2016).

To investigate the interactive effects of extreme drought events and nutrient addition (NPK), we established a field experiment at the UFZ Experimental Research Station (Bad Lauchstädt, Germany), which combines the treatments of two globally distributed networks – the Drought-Network and the Nutrient Network (Borer *et al.*, 2014). Here, we tested the responses of soil microorganisms, nematodes, and soil mesofauna to the interactive effects of extreme drought and nutrient addition (NPK) across all seasons. Based on prior research, we hypothesized that (1) drought will reduce the activity of soil organisms, whereas (2) nutrient addition will increase their activity, owing to enhanced plant litter input that subsequently increases resource availability for soil organisms. Furthermore, we predicted that (3) the interactive effects of drought and nutrient addition will result in detrimental conditions for soil organisms as the negative effects of drought were expected to be further enhanced by increased plant growth under nutrient addition, resulting in reduced soil water availability for soil organisms.

Methods

i. Research site

The study site is located at the Experimental Research Station of the Helmholtz Centre for Environmental Research (UFZ), which is situated in Bad Lauchstädt, Germany. The field site is located in the central German dry area with a mean annual precipitation of 487 mm and an average annual daily temperature of 8.9°C (Meteorological data of Bad Lauchstädt, Helmholtz Centre for Environmental Research GmbH - UFZ, Department of Soil System Science, 1896-2017). The area represents an anthropogenic grassland, which is maintained by moderate mowing (twice a year since 2012). It is a successional plant community dominated by *Vulpia myuros* (L.) C. C. Gmel., *Picris hieracoides* (L.) and *Taraxacum officinale* (F. H. Wigg.) with *Apera spica-venti* (L.) P. Beauv. and *Cirsium arvense* (L.) Scop. being very common. The soil is classified as a haplic chernozem, developed upon carbonatic loess substrates, distinguished by a composition of 70% silt and 20% clay (Altermann *et al.*, 2005).

ii. Weather conditions

Weather conditions within the two-year sampling period of this study were in line with the long-term average despite some exceptions: precipitation patterns deviated from the long-term average in 2016 with a dry May (21.2 mm compared to 62.3 mm of the long-term record from 2005-2015) and a wet June (80.2 mm compared to 41.2 mm of the long-term record from 2005-2015). September tended to be dryer than usual in both years (19.5 mm in 2016 and 22.1 mm in 2017 compared to 51.8 mm of the long-term record from 2005-2015).

iii. Experimental design and treatments

The experimental site was established in March 2015; both treatments were applied for the first time in March 2016. The experimental design consists of five blocks with five plots each. The plots have a size of 2 x 2 m and are arranged at a distance of 3 m from each other (Fig. S1). The experiment includes two treatments with two levels each: a drought and a fertilization treatment (NPK addition), as well as their interaction (drought x NPK). Notably, this experiment crosses treatments of two globally distributed experimental networks: the full NPK fertilization treatment of the Nutrient Network (Borer *et al.*, 2014) and the drought treatment of the Drought-Network (http://www.drought-net.colostate.edu/).

In order to simulate drought, a rainfall manipulation system was established (Yahdjian and Sala, 2002) using corrugated acrylic strips. The roofs have a size of 3 x 3 m and reduce precipitation by 55% throughout the year, simulating a severe long-term reduction in precipitation. Roofs were built with a slope of 20° to ensure water runoff and account for the expected snow load in the region. Exclusion of potential artefacts was realized by equal roof constructions using inverted acrylic strips conceived to let rainfall pass (Vogel *et al.*, 2013) (Fig. S2). To control for possible infrastructure effects of the roof constructions itself, a fifth plot was added to each block without any roof construction (ambient plots), thus receiving ambient precipitation (not crossed with the fertilization treatment and thus not part of this study, see Fig. S1). In order to validate the drought treatment, soil water content was examined for all plots and every sampling campaign. All three precipitation levels differed significantly in their soil water content (Tukey's HSD test, $p < 0.05$): as intended, the lowest soil water content was found for the drought treatment (-19.4% compared to the ambient plots). Also the infrastructure control plots (with concave roof constructions) differed significantly from the ambient plots (without roof construction), indicating that there were effects of the roof construction itself (-13.4%). Furthermore, soil water content varied significantly between seasons (Table S1; Fig. S3).

140 The fertilization treatment was realized by annual NPK addition (applied at 10 g m^{-2} y^{-1} by elemental mass)
141 before the growing season. In addition, the micronutrient mix "Micromax Premium" (Everris) was applied
142 in the first treatment year (Borer *et al.*, 2014).

143

144 ### iv. Soil sampling

145 The first soil sampling took place in March 2016. Sampling campaigns were repeated every three months
146 to cover every season (spring, summer, fall, winter) from March 2016 to December 2017 (i.e., eight
147 samplings across two years). Samples were taken on all plots with roof construction (drought and control)
148 with a steel core sampler (1 cm in diameter; 15 cm deep). Seven subsamples per plot were homogenized,
149 sieved at 2 mm, and stored at 4°C. Soil samples were used to determine soil water content and microbial
150 respiration. In addition, nematodes were extracted from the soil samples in spring and summer of 2017
151 (Ruess, 1995).

152

153 ### v. The Bait Lamina Test

154 Feeding activity of soil invertebrates was surveyed using the bait lamina test (Terra Protecta GmbH, Berlin,
155 Germany), which presents a commonly used rapid ecosystem function assessment method (Kratz, 1998).
156 The test uses rigid PVC sticks (1 mm x 6 mm x 120 mm) with 16 holes of 1.5 mm diameter in 5 mm distance.
157 Original sticks were filled with a bait substrate consisting of 70% cellulose powder, 27% wheat bran, and
158 3% activated carbon, which was prepared according to the recommendations of Terra Protecta. The bait
159 substrate is primarily consumed by mites, collembolans, nematodes, enchytraeids, millipedes, and
160 earthworms, whereas microbial activity plays a minor role in bait loss (Hamel *et al.*, 2007; Gardi *et al.*,
161 2009; Rożen *et al.*, 2010; Simpson *et al.*, 2012). The sticks were inserted vertically into the soil with the

topmost hole just below the ground surface. In order not to damage the sticks, a steel knife was used to prepare the ground prior to insertion. Five sticks were used per plot to account for some spatial heterogeneity (Thakur *et al.*, 2018). For each sampling campaign, the bait lamina sticks were removed from the soil after three weeks of exposure and directly evaluated in the field. Bait consumption was recorded as empty (1), partly empty (0.5), or filled (0). Thus, soil invertebrate feeding activity could range from 0 to 16 (maximum feeding activity). Mean bait consumption per plot was calculated prior to statistical analyses.

vi. Respiration measurements

An O_2-microcompensation system was used to measure the respiratory response of soil microorganisms (Scheu, 1992). First, basal respiration was determined as a measure of soil microbial activity (µl O_2 h^{-1} g^{-1} soil dry weight). Second, the maximal respiratory response after the addition of glucose (4 mg g^{-1} dry weight soil, solved in 1.5 ml distilled water) allowed us to determine microbial biomass (µg Cmic g^{-1} soil dry weight) (Anderson and Domsch, 1978).

vii. Nematode analysis

Nematode extraction was conducted with a modified Baermann method (Ruess, 1995). Approximately 25 g of soil per plot were transferred to plastic vessels with a milk filter and a fine gaze (200 µm) at the bottom and placed in water-filled funnels. More water was added to saturate the soil sample and to ensure a connected water column throughout the sample and the funnel. Hence, nematodes migrated from the soil through the milk filter and the gaze into the water column and gravitationally-settled at the bottom of a closed tube connected to the funnel. After 72 h at 20°C, the nematodes were transferred to

184 a 4% formaldehyde solution. Nematodes were counted at 100x magnification using a Leica DMI 4000B
185 light microscope. Identification was conducted at 400x magnification. For identification, sediment
186 material from the bottom of each sample vial was extracted with a 2 ml plastic pipette and examined in
187 temporary mounted microscope slides. At least 100 well-preserved specimens (if available in the sample)
188 were randomly selected and identified to genus (adults and most of the juveniles) or family level
189 (juveniles), following Bongers (1988). Nematode taxa were then arranged into trophic groups (bacteria-,
190 fungal- and plant-feeders, omnivores and predators) (Yeates *et al.*, 1993; Okada *et al.*, 2005). Due to low
191 overall densities, omnivorous and predatory nematodes were grouped into a combined feeding type for
192 most analyses. Nematodes were also ordered according to the colonization-persistence gradient (c-p
193 values) (Bongers, 1990; Bongers and Bongers, 1998). The colonizer-persistence scale classifies nematode
194 taxa based on their life history strategy (i.e. r or K strategists). Cp-1 taxa are distinguished by their short
195 generation cycles and high fecundity. They mainly feed on bacteria. Cp-2 taxa have longer generation
196 times, lower fecundity and consist of bacterivores and fungivores (Ferris et al., 2001). Both are categorized
197 as r-strategists. Cp-3 to cp-5 are classified as K-strategist nematodes with longer generation times, higher
198 trophic feeding levels and increasing sensitivity against disturbances (Ferris et al., 2001). The c-p-values
199 can be used to calculate the Maturity Index (MI) as weighted means of nematode families assigned to c-
200 p-values. It is used to describe soil health and as an indicator of overall food web complexity (Bongers,
201 1990; Bongers and Bongers, 1998).

202 $$MI = \sum_{i=1}^{n} \binom{n}{k} v\,(i) * f(i)$$

203 with *v(i)* being the c-p-value of a taxon i and *f(i)* being the frequency of that taxon in a sample.

204 Furthermore, nematode taxa were assigned to functional guilds according to Ferris *et al.* (2001), which
205 then served as a basis to calculate additional indices. Functional guilds refer to the following trophic

206 groups: bacterial feeders (Ba_X), fungal feeders (Fu_X), omnivores (Om_X), and carnivores (Ca_X). Associated
207 numbers (i.e., the x of the respective trophic group) are again referring to the c-p values described above.
208 The Enrichment Index (EI) indicates the responsiveness of the opportunistic bacterial (Ba_1 and Ba_2) and
209 fungal feeders (Fu_2) to food web enrichment (Ferris *et al.*, 2001) and is calculated as follows:

210 $$\mathrm{EI} = 100 \times [\frac{\mathrm{e}}{\mathrm{e+b}}]$$

211 with *e* as weighted frequencies of Ba_1 and Fu_2 and *b* as weighted frequencies of Ba_2 and Fu_2 nematodes
212 (Ferris *et al.*, 2001). The Channel Index (CI) reflects the nature of decomposition channels through the soil
213 food web. High values indicate a predominant decomposition pathway of organic matter dominated by
214 fungal-feeding nematodes, whereas low values refer to bacterial-dominated decomposition pathways
215 (Ferris *et al.*, 2001).

216 $$\mathrm{CI} = 100 \times [0.8 \times \frac{\mathrm{Fu2}}{3.2 \times \mathrm{Ba1} + 0.8 \times \mathrm{Fu2}}]$$

217 with 0.8 and 3.2 representing enrichment weightings for Fu_2 and Ba_1 nematodes (Ferris *et al.*, 2001). The
218 Structure Index (SI) provides information about the complexity of the soil food web. A highly structured
219 food web with a high SI suggests ecosystem stability, while low values imply environmental disturbance
220 (Ferris *et al.*, 2001).

221 $$\mathrm{SI} = 100 \times [\frac{\mathrm{s}}{\mathrm{s+b}}]$$

222 with *s* calculated as the weighted frequencies of Ba_3-Ba_4, Fu_3-Fu_4, Ca_3-Ca_5 and Om_3-Om_5 nematodes, and
223 *b* representing the weighted frequencies of Ba_2 and Fu_2 nematodes (Ferris *et al.*, 2001).

224

225 ### i. Statistical analyses

226 Linear mixed effects models were used to analyze the treatment effects (drought and NPK fertilization)
227 on invertebrate feeding activity, microbial activity and microbial biomass using the R-package "*nlme*"
228 (Pinheiro *et al.*, 2017). The random intercept of the model was structured with plots nested within blocks,
229 which were nested within year (year as a categorical factor). To account for repeated measurements
230 within plots, we compared first-order autoregressive and compound symmetry covariance structures
231 based on the Akaike information criterion (AIC). As differences between AIC values were lower than 2, the
232 simplest covariance structure (i.e. compound symmetry) was used. Based on the importance of soil water
233 content for microbial activity and biomass (Wan *et al.*, 2007), soil water content was added as an
234 additional explanatory variable in the linear mixed effects models (Table S3-4, Fig. S4-5). As we were
235 expecting a strong relation between aboveground live plant biomass and microbial biomass (Kent and
236 Triplett, 2002), plant biomass served as an additional explanatory variable in the models (Table S5, Fig.
237 S6). Model assumptions were checked by visually inspecting residuals for homogeneity and Pearson
238 residuals for normality. Based on that, invertebrate feeding activity and microbial activity were log-
239 transformed (log(x+1)) to meet the assumptions of the model. Linear mixed effects models were also used
240 to assess the effects of drought, NPK fertilization, season (spring and summer 2017), and their interactions
241 on nematode richness, total density, trophic groups, and indices. For all nematode analyses a random
242 intercept with plots nested within bock was included in the models. In addition, we accounted for the
243 repeated measurements within plots by using a compound symmetry covariance structure, which fitted
244 the data better than a first-order autoregressive covariance structure based on the Akaike information
245 criterion. To evaluate model variation explained by fixed and random effects, marginal and conditional R^2
246 were calculated using the "*MuMIn*" package (Barton, 2018); marginal R^2 represents model variation
247 explained by fixed effects in the final model and conditional R^2 represents model variation explained by
248 both random and fixed effects. Graphs are based on mixed effects model fits for each treatment that were

extracted using the package "*ggeffects*" (Lüdecke, 2018). All statistical analyses were conducted using R version 3.4.2 (R Core Team, 2017).

Results

i. Soil microbial responses

Soil microbial activity ranged from 0.7 to 5.1 µl O_2 h^{-1} g^{-1} dry weight soil with an average of 1.7 µl O_2 h^{-1} per g dry weight soil across all measurements. We could not detect a significant effect of the drought or the fertilization treatment on soil microbial activity (Fig. 1a). However, microbial respiration was significantly affected by season, with lowest activity in summer and highest activity in winter (Table 1; Fig. 1b). In addition, we found a positive relation between microbial activity and soil water content ($F_{1, 111}$ = 170.83; $p < 0.001$, Table S3) that was independent of the drought and fertilization treatment (Fig. S4).

Soil microbial biomass ranged from 168.0 to 979.8 µg Cmic g^{-1} dry weight soil with an average of 530.6 µg Cmic g^{-1} dry weight soil across all measurements. Overall, soil microbial biomass increased significantly with NPK fertilization (Fig. 1c). Microbial biomass was also significantly affected by season with lowest biomass in summer and highest biomass in fall (Fig. 1d, Table 1). Furthermore, fertilization and soil water content interactively affected microbial biomass ($F_{1, 111}$ = 10.57, $p = 0.002$, Table S4) – whereas microbial biomass increased with higher soil water content under ambient conditions, it slightly decreased with higher soil water content on plots with NPK fertilization (Fig. S5). In addition, soil microbial biomass increased significantly with aboveground live plant biomass ($F_{1, 59}$ = 8.81; $p = 0.004$, Table S6, Fig. S5).

ii. Nematode responses

Neither total nematode density nor richness were significantly affected by any of the experimental treatments (Fig. 2a-b, Table 2); we could only detect significant differences between the sampling campaigns (Fig. S7a-b). Among the nematode trophic groups, only bacteria-feeders were significantly increased by the fertilization treatment (Fig. 2c), which was mainly due to an increase of the r-strategic

Ba_1-nematodes (Fig. S8a). In addition, bacteria-feeders represented a higher proportion in the samples collected in summer (Fig. S7c). Plant-feeders were affected by the interactive effects of fertilization and season: whereas NPK favored plant-feeding nematodes in spring, it had a negative effect in summer (Fig. 2d and S7d). Fungal-feeders and the combined group of omnivorous and predatory nematodes were not significantly affected by any of the treatments (Fig. 2e-f, Table 2). However, a closer look at changes in the nematode community composition revealed that nematodes with higher c-p values, in detail Fu_3-nematodes (Fig. S8e), Om_4-nematodes (marginally significant, Fig. S8g), cp3 (marginally) and cp4-nematodes (Fig. 9d and 9f) decreased significantly in response to fertilization, whereas cp2 plant-feeding nematodes only decreased with fertilization under ambient precipitation, but increased with fertilization under drought conditions (Fig. S9c, Table S6). Ba_4-nematodes significantly increased under drought conditions (Fig. S8c).

While the Enrichment Index increased marginally significantly under drought conditions (Table 2; Fig. 3a), the Structure Index and the Maturity Index were marginally significantly decreased by drought (Fig. 3b-c). Fertilization increased the importance of the bacterial decomposition channel as indicated by a marginally significant decrease of the Channel Index (Fig. 3d). In addition, fertilization decreased nematode complexity as indicated by a significant decrease of the Structure and Maturity Index. (Fig. 3b-c). Furthermore, plotting the EI-SI profile of the nematode community grouped by the different treatment combinations depicted that whereas some of the control and drought plots could be found in quadrant C (undisturbed, moderate enrichment, structured food web), nearly all NPK and NPK x drought plots were located in quadrant D (stressed, depleted, degraded food web) or in quadrant A (high disturbed, enriched, disturbed food web) (Fig. 3e).

iii. Soil invertebrate feeding responses

296 Mean soil invertebrate feeding activity per plot ranged from 0 to 60% of consumed bait substrate with an
297 average of 11% bait consumption. Feeding activity was significantly affected by an interactive effect of
298 drought x fertilization; overall, nutrient addition decreased invertebrate feeding activity at ambient
299 precipitation, but had no significant effect under drought conditions (Fig. 4a). These treatment effects
300 were consistent across seasons (no treatment x season interaction), however, the level of soil invertebrate
301 feeding activity varied strongly between seasons and tended to be highest in summer and strongly
302 decreased in winter (Table 1; Fig. 4b).

303 Table 1: F-values (num d.f., denom d.f.) of linear mixed effects models for the effects of drought, NPK
304 fertilization, season, and their interactions on soil invertebrate feeding activity (log-scaled), soil microbial
305 activity (log-scaled), and soil microbial biomass. A random intercept with plots nested within blocks, which
306 were nested within year was added to the model. A compound symmetry covariance was used to account
307 for repeated measurements within plots. Marginal R^2: model variation explained by fixed effects;
308 conditional R^2: model variation explained by both fixed and random effects. NPK = NPK fertilization. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$
309

Response Variables	**Drought**	**NPK**	**Season**	**Drought x NPK**	**Drought x Season**	**NPK x Season**	**Drought x NPK x Season**	**R^2 (marg./cond.)**
	F-value (1,27)	*F-value (1,27)*	*F-value (3,108)*	*F-value (1,27)*	*F-value (3,108)*	*F-value (3,108)*	*F-value (3,108)*	
Invertebrate feeding activity	22.65***	22.60***	22.78***	9.17**	0.19	0.36	0.38	0.44/0.49
Microbial activity	0.78	2.71	31.02***	0.02	1.07	0.30	0.28	0.37/0.49
Microbial biomass	2.25	35.48***	3.95*	0.22	1.55	0.92	0.36	0.084/0.80

310

311

Table 2: F-values (num d.f., denom d.f.) of linear mixed effects models for the effects of drought, fertilization, sampling, and their interaction on soil nematode response variables. Two sampling campaigns (spring and summer 2017) were included. Plots nested within blocks served as a random intercept in the model. A compound symmetry covariance was used to account for repeated measurements within plots. Marginal R^2: model variation explained by fixed effects; conditional R^2: model variation explained by both fixed and random effects. NPK = NPK fertilization. $^{(*)}$ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Nematode response variable	**Drought**	**NPK**	**Sampling**	**Drought x NPK**	**Drought x Sampling**	**NPK x Sampling**	**Drought x NPK x Sampling**	**R^2 (marg./cond.)**
	F-value (1,12)	*F-value (1,12)*	*F-value (1,16)*	*F-value (1,12)*	*F-value (1,16)*	*F-value (1,16)*	*F-value (1,16)*	
Total density	0.278	2.027	64.065***	0.517	0.022	1.833	0.831	0.60/0.77
Richness	0.224	0.622	40.602***	0.224	0.156	0.029	0.003	0.50/0.65
Enrichment Index	3.304 $^{(*)}$	0.840	0.067	0.000	0.025	0.046	0.171	0.094/0.18
Structure Index	4.949 $^{(*)}$	6.645*	0.017	0.320	1.699	0.513	0.530	0.23/0.29
Channel Index	1.601	3.982 $^{(*)}$	1.418	0.035	1.624	0.000	0.109	0.19/0.50
Maturity Index	5.073 $^{(*)}$	10.179**	0.000	0.515	1.987	0.207	0.722	0.28/0.34
Plant feeders	0.070	0.466	6.605*	0.885	1.307	5.952*	0.861	0.19/0.76
Fungal feeders	0.500	0.421	0.243	0.333	0.658	0.329	0.425	0.063/0.32
Bacteria feeders	0.046	5.319*	5.319**	0.776	1.968	1.315	1.865	0.39/0.47
Predators/Omnivores	2.355	2.171	0.199	0.238	0.113	2.094	0.961	0.17/0.28

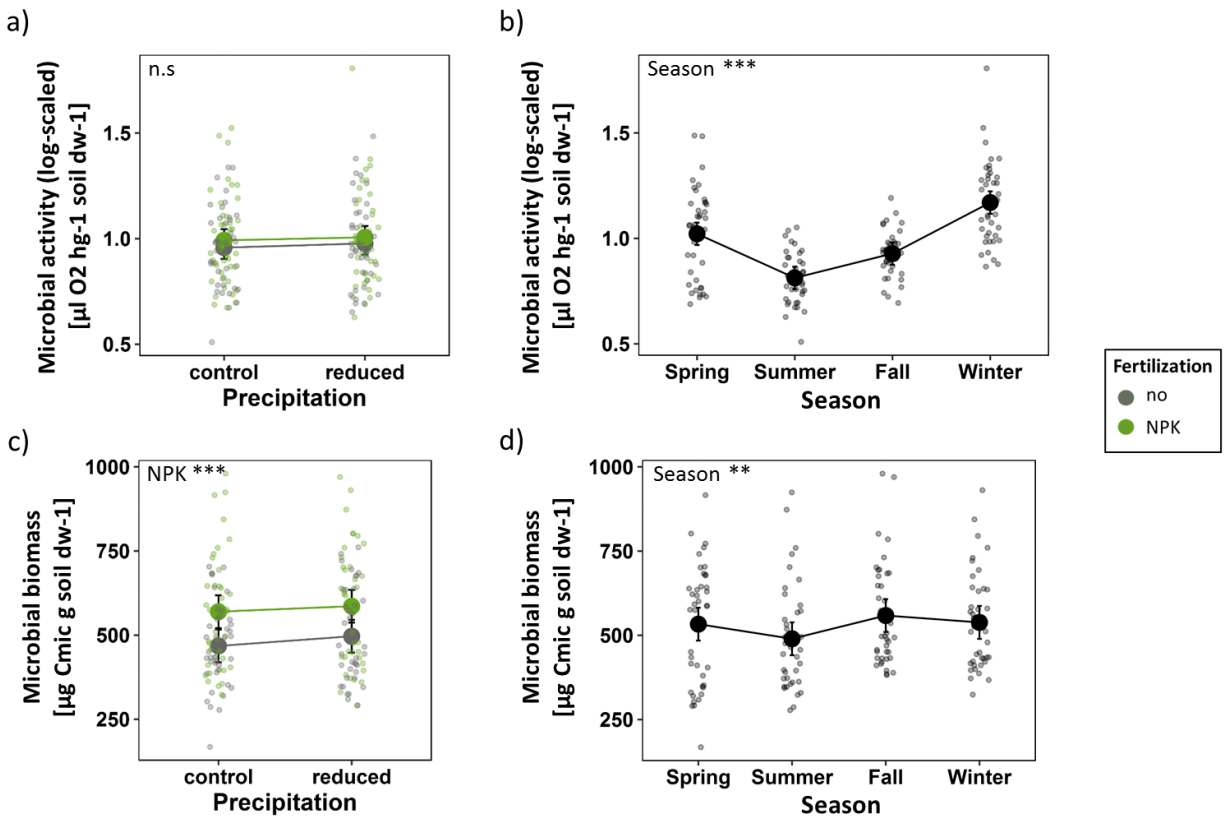

Fig 1: The effects of drought, NPK fertilization, and season on soil response variables based on mixed effects model fits for each treatment. (a) Combined treatment effects across all seasons and (b) seasonal effects on soil microbial activity (log-scaled). (c) Combined treatment effects across all seasons and (d) seasonal effects on soil microbial biomass. Error bars indicate 95% confidence intervals. Grey = no NPK fertilization; green = NPK fertilization.

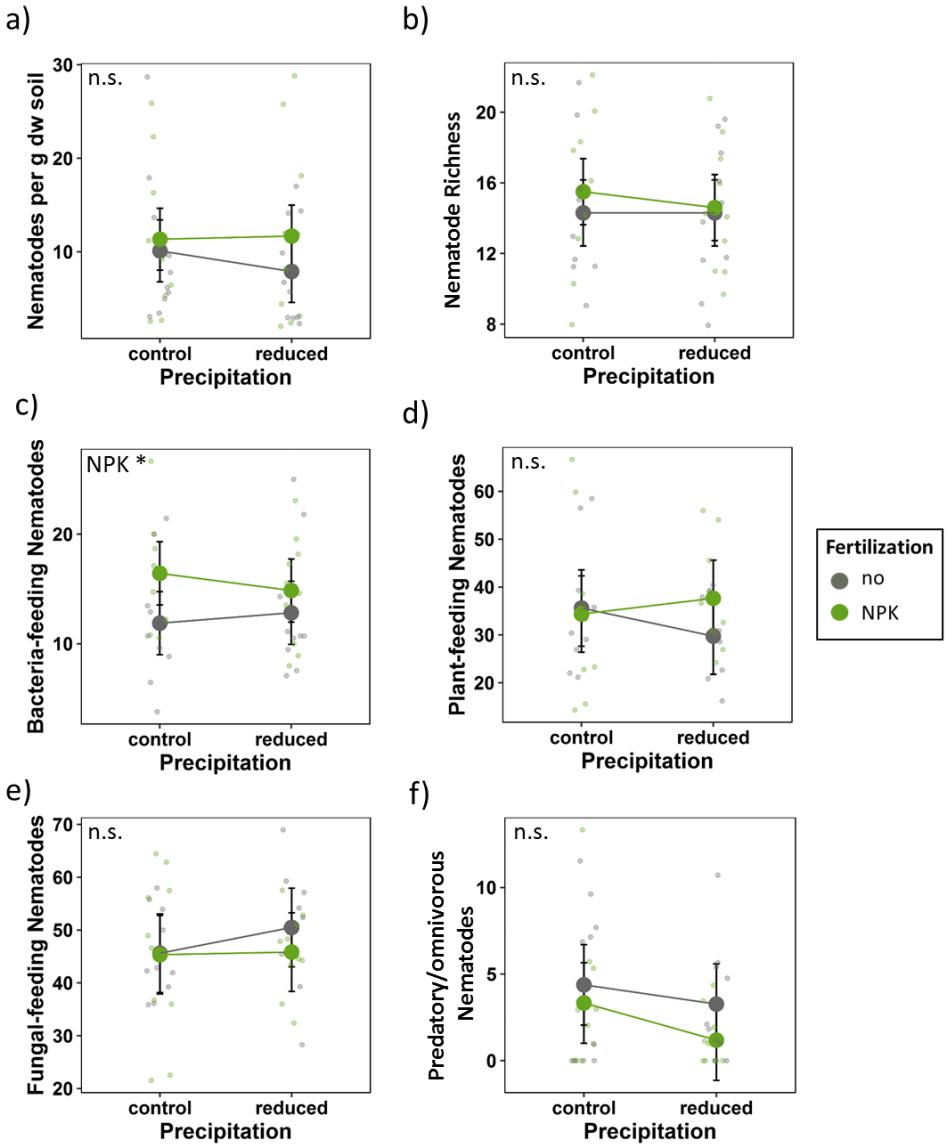

Fig 2: The effects of drought and NPK addition on nematode response variables based on mixed effects model fits for each treatment. (a) Total nematode density per g dry weight soil; (b) nematode taxon richness; (c) bacteria-feeding nematodes; (d) plant-feeding nematodes; (e) fungal-feeding nematodes; and (f) predatory- and omnivorous nematodes. Error bars indicate 95% confidence intervals. Grey = no NPK fertilization; green = NPK fertilization. Both seasons (spring and summer 2017) are included (see Fig. S7 for sampling effects).

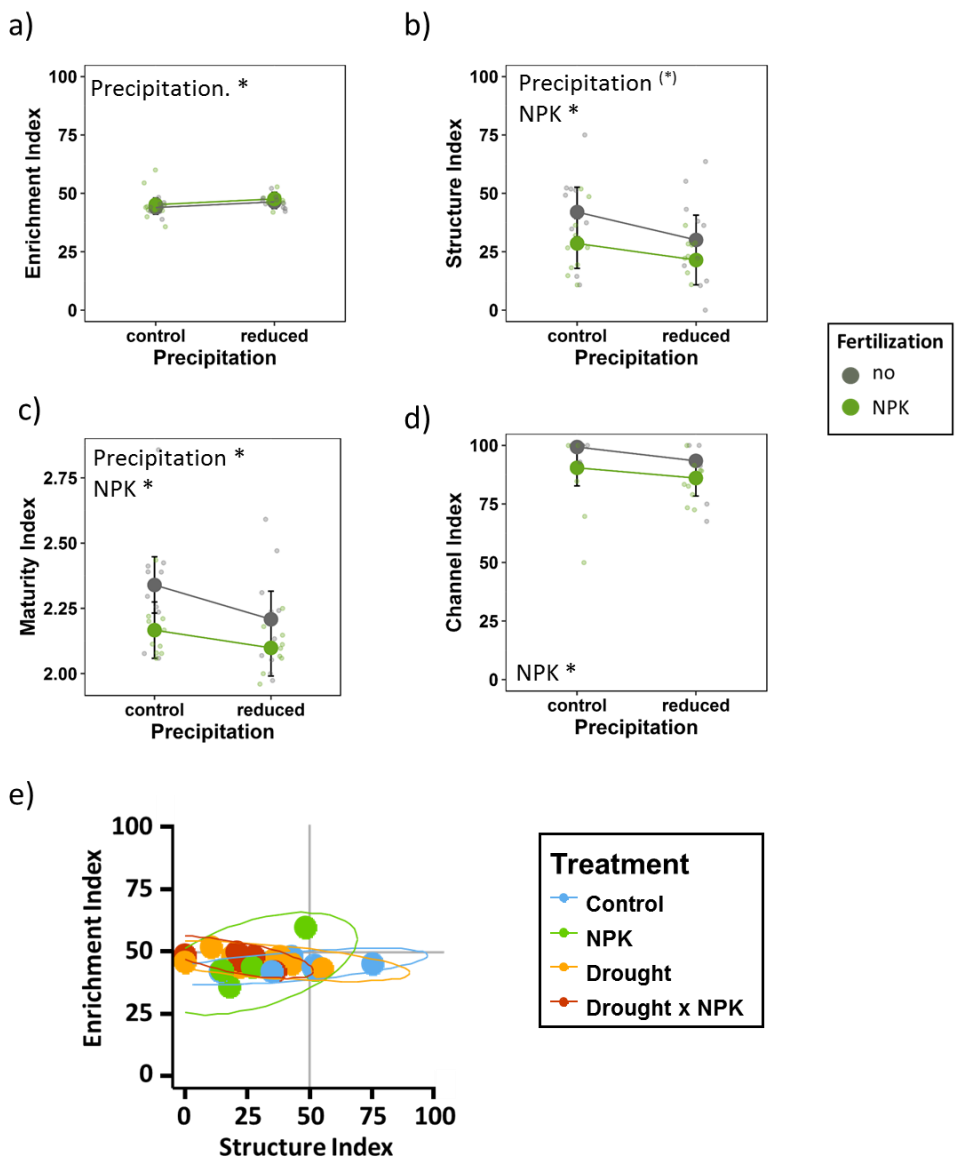

Fig 3: The effects of drought and NPK addition on soil nematode indices based on mixed effects model fits for each treatment. (a) Enrichment Index; (b) Structure Index; (c) Maturity Index, and (d) Channel Index. Error bars indicate 95% confidence intervals. Grey = no NPK fertilization; green = NPK fertilization. (e) Enrichment Index (EI) and Structure Index (SI) trajectories for all plots according to the treatment combinations. Blue = control; green = NPK fertilization; yellow = drought; red = drought x NPK. Ellipses group treatments. Both seasons (spring and summer 2017) are included.

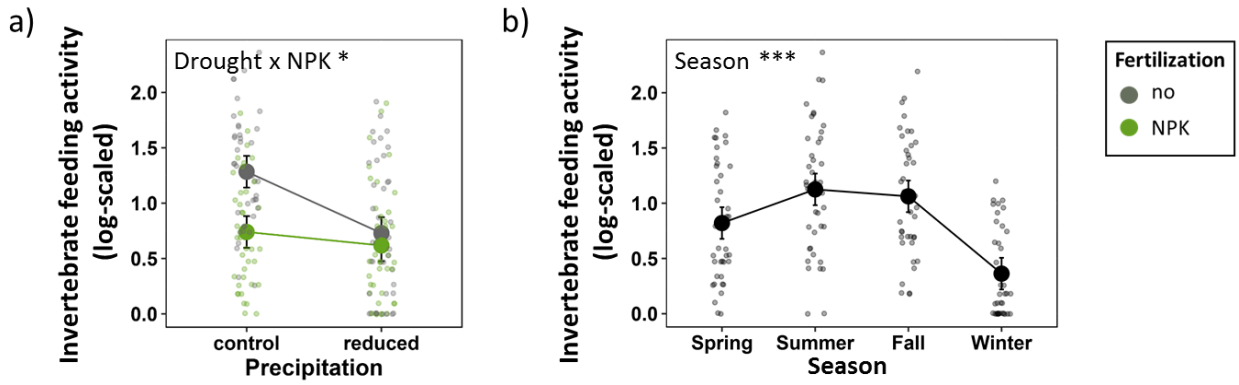

Fig. 4: The effects of drought, NPK fertilization, and season on soil invertebrate feeding activity (log-scaled) based on mixed effects model fits for each treatment. (a) Combined treatment effects across all seasons and (b) seasonal effects. Error bars indicate 95% confidence intervals. Grey = no NPK fertilization; green = NPK fertilization.

Discussion

We studied the impacts of two major global change drivers, namely drought and nutrient enrichment, on soil communities and functions. In order to obtain a comprehensive picture of how soil ecosystem processes are affected by these drivers, we investigated the responses of a wide range of soil organisms across all seasons within a two-year timeframe. Intriguingly, we saw vastly differing responses among trophic levels.

Our first hypothesis, predicting detrimental effects of drought on soil organisms, was confirmed to some extent: drought reduced soil invertebrate feeding activity and led to a more disturbed soil nematode community structure, whereas soil microbial activity and biomass were not significantly affected. The dependency of soil invertebrates on soil moisture content is well documented (Coleman *et al.*, 2004) as is the fact that soil microfauna is more prone to water stress than bacteria and fungi (Manzoni *et al.*, 2012). The detrimental drought effects on faunal activity are thus in line with previous studies, which claim that abiotic conditions are shaping the performance of the soil faunal community (Briones *et al.*, 1997). Microarthropods (mites and collembolans), enchytraeids, and earthworms are some of the most relevant groups found in the upper soil layer in temperate regions (Gardi *et al.*, 2009) and are likely to account for most of the feeding activity leading to bait perforation (Helling *et al.*, 1998; Gongalsky *et al.*, 2008). Extreme drought not only forces them to migrate to deeper soil layers, but also interferes with their reproduction and development success, which is possibly the reason why they are highly susceptible to drought (Siepel, 1996; Frampton *et al.*, 2000; Wever *et al.*, 2001; Maraldo and Holmstrup, 2010). Furthermore, drought conditions entail drier food sources for detritivores, which are more difficult to digest (Thakur *et al.*, 2018).

372 In line with our expectations, drought was also responsible for (moderate) shifts in nematode indices. The
373 environmental conditions were changed towards an enriched, more disturbed, less structured system,
374 with a higher proportion of opportunistic nematodes. Already at ambient precipitation levels, the guilds
375 of the opportunistic Fu_{2-} and Ba_2-nematodes accounted for the highest shares at our experimental site,
376 indicating a basal food web that is capable to cover a wide ecological amplitude and is already adapted to
377 some environmental stress (Ferris *et al.*, 2001). The positive response of the Enrichment Index to drought
378 suggests mortality at higher trophic levels, which subsequently promoted nutrient enrichment and gave
379 further rise to opportunistic nematodes (Ferris *et al.*, 2001). Thus, overall, drought led to simplified trophic
380 structures of the nematode community.

381

382 In contrast to our initial hypothesis, soil microbial activity and biomass were not affected by the drought
383 treatment. This was unexpected given the intensity of the drought treatment applied within the
384 experiment (precipitation was reduced by 55% during the entire study period) and the fact that most soil
385 microbes are strongly dependent on high soil moisture levels (Griffiths *et al.*, 2003; Wan *et al.*, 2007).
386 However, our results indicate that drought may not be a strong determinant of soil microbial activity and
387 biomass at the study site. This is in line with Pailler *et al.* (2014), who found microbial functional responses
388 to be robust against drought. In spite of the negligible responses to the drought treatment, we could
389 reveal that soil water content explained a significant proportion of the variability in microbial activity, yet
390 irrespective of the treatments. This suggests that microorganisms residing in the upper soil layer are highly
391 depending on soil moisture levels and must therefore be able to sustain drought periods, for instance
392 through physiological modifications. Such adaptations may comprise an adjustment of internal water
393 potential, sporulation, or production of exopolysaccharides that provide protection against exsiccation
394 (Harris, 1981; Roberson and Firestone, 1992). Apart from the resilience of the microbial community
395 against experimental drought, we observed distinct variation of microbial activity and biomass across

396 seasons. This provides evidence that temporal environmental variability is a strong predictor of species
397 activity and emphasizes the dependency of soil organisms on seasonal patterns (Deng *et al.*, 2010;
398 Sorensen *et al.*, 2013; Tonkin *et al.*, 2017). We therefore infer that seasonal fluctuations in natural
399 precipitation may have led to acclimatization of the microbial communities to drought periods as they are
400 part of their climatic history (Waldrop and Firestone, 2006; Cruz-Martínez *et al.*, 2009), which may explain
401 the weak effects of the experimentally induced drought.

402

403 The responses of soil biota were again ambiguous with regard to our second hypothesis, in which we
404 expected nutrient enrichment to promote the activity of soil biota. Consistent with our hypothesis, soil
405 microbial biomass increased under fertilization. Soil invertebrate feeding activity, however, substantially
406 declined under elevated nutrient supply, questioning the universal validity of our initial hypothesis. The
407 pronounced responsiveness of soil microbial biomass to NPK fertilization is in line with similar studies
408 reporting positive effects of nitrogen fertilization on microbial biomass and changes in microbial
409 community structure and function (Campbell *et al.*, 2010; Cusack *et al.*, 2011). Fertilization certainly
410 enhanced nutrient availability, resulting in higher yields of aboveground plant biomass (Berger *et al.,* in
411 prep.), which is often accompanied by an expanded root system (Stevens *et al.*, 2015). Subsequently, this
412 increases the release of organic compounds into the soil (Bais *et al.*, 2006), providing substrates that
413 support the growth of microbial communities towards higher population densities (Kent and Triplett,
414 2002).

415

416 Also nematode indices were highly responsive to NPK fertilization, resulting in a less structured and more
417 disturbed system with an enhanced bacteria-driven decomposition pathway. The latter was additionally
418 supported by a strong increase in bacteria-feeding nematodes (especially Ba_1) and an equally strong

419 decrease in fungal-feeding nematodes (Fu_3) under fertilization, indicating that fertilization had
420 detrimental effects on soil fungi. This is in line with the general notion that fertilization favors bacteria-
421 dominated decomposition (Wardle and Yeates, 1993; Ferris *et al.*, 2001; Kardol *et al.*, 2010; Song *et al.*,
422 2016). The simplification of the nutrient-enriched soil food web is also reflected by declines of the
423 omnivorous nematodes (Om_4) and the cp3 and cp4 nematodes, which consist of long-living, pollutant
424 sensitive, rather immobile organisms that are prone to environmental stress (Bongers and Bongers, 1998).
425 When linking these changes reported for the nematode indices to the responses of the microbial
426 community, our results suggest that fertilization promoted the growth of bacteria (simultaneously
427 repressing fungi), which then accounted for a strong increase in microbial biomass. As a result, this
428 restructuring of the microbial community has thus provided the basis for the observed increase in
429 bacteria-feeding nematodes and some of the shifts in nematode indices.

430

431 Current evidence on soil invertebrate responses to fertilization is equivocal. Several studies reported an
432 enhancing effect of fertilization on soil invertebrate activity and diversity (Graenitz and Bauer, 2000; Van
433 der Wal *et al.*, 2009), whereas others revealed no such effects (Maraun *et al.*, 2001; Lindberg *et al.*, 2002),
434 or recorded declines in soil fauna abundances and diversity after fertilizer application (Gardi *et al.*, 2009).
435 Most likely, the diminished feeding activity of soil invertebrates can be explained by alterations of soil
436 physicochemical properties. Fertilization often results in reduced soil pH, which is negatively correlated
437 with the abundance of most soil invertebrates (Kaneko and Kofuji, 2000; Wang *et al.*, 2015b). Especially
438 earthworms, which represent a significant part of soil invertebrates' biomass (Fierer *et al.*, 2009), have
439 been reported to decline noticeably in numbers under reduced soil pH (Gudleifsson, 2002). In addition to
440 this direct effect, the observed shifts in nematode indices could provide evidence of possible indirect
441 effects on invertebrate feeding activity: as fungi seemed to be substantially reduced by fertilization,
442 microarthropods like Collembola and Oribatid mites, which are strongly depending on fungi, may thereby

443 be deprived of their main food source (Kaneko *et al.*, 1995; Maraun *et al.*, 2001). As a consequence, they
444 are presumably also declining in their abundances, thus limiting their possible contribution to bait
445 perforation. Overall, environmental constraints, such as reduced soil pH in combination with altered
446 energy channels and simplified food web structures, outweighed potential positive bottom-up effects
447 through enhanced plant growth, which we expected to find.

448

449 Prior studies emphasized the importance of interactive effects of global change drivers as they will
450 profoundly alter ecosystem functions and services (Eisenhauer *et al.*, 2012; Zhou *et al.*, 2016). Accordingly,
451 our third hypothesis predicted nutrient addition to reinforce drought effects, resulting in aggravated living
452 conditions for soil organisms. Indeed, drought and fertilization interacted significantly in restraining soil
453 invertebrate feeding activity, partially supporting our hypothesis. However, as discussed above,
454 fertilization obviously created an unfavorable environment for most soil invertebrates at our site.
455 Although both global change drivers individually decreased soil invertebrate feeding activity, the
456 interaction, however, did not result in further declines. We therefore conclude that the combined effects
457 may have led to a distinct restructuring of the soil faunal community by promoting species better adapted
458 to adverse conditions, and thus revealing no measurable change in net effects. Since the combined global
459 change drivers are likely to modify aboveground plant communities (Gough *et al.*, 2000; Thuiller *et al.*,
460 2005; Bobbink *et al.*, 2010), alterations in the quality of aboveground litter inputs can be expected. Leaf
461 litter quality, in turn, affects soil fauna and might therefore be responsible for reshaping the faunal
462 community (Cornwell *et al.*, 2008; Carrillo *et al.*, 2012). With the methods applied in our study, however,
463 we can only speculate about potential changes in the soil faunal community composition. This highlights
464 the need for future research to detect which specific groups are responsible for bait perforation. This
465 could be done, for instance, by exposing bait lamina strips with a labelled substrate under controlled
466 laboratory conditions (Briones *et al.*, 2001; Dyckmans *et al.*, 2005). Building on that, the abundances of

467 the most important groups of soil organisms could be monitored in the field, while being exposed to
468 different global change drivers.

469

470 In contrast to the invertebrate feeding activity, microbial activity was not significantly affected by the
471 interaction of the two global change drivers. Moreover, we could not detect any interactive effects on
472 nematode indices or nematode groups, except for the highly tolerant cp2 plant feeding nematodes that
473 increased in abundance under the most disturbed environmental conditions (drought x NPK) and could
474 have possibly benefited from enhanced plant biomass. This illustrates the robustness of a large portion of
475 the soil community to interactive global change effects, which might therefore be able to buffer
476 prospective global change effects to a certain extent.

477

478 In conclusion, the main groups of soil organisms investigated in the present study responded differently
479 to interacting global change drivers. Soil invertebrate activity was strongly impaired by both global change
480 drivers and their interaction, while microbial biomass benefited from enhanced nutrient availability, and
481 microbial activity was surprisingly unaffected by all treatments. Despite the strong seasonal dynamics of
482 temperate regions, these treatment effects remained constant across all seasons within two years.
483 Notably, nematode indices pointed to changes in the state of the ecosystem, shifting towards simplified
484 and more disturbed systems under drought and especially under nutrient addition that mostly facilitated
485 opportunistic species. We could show that soil biota differ considerably in their sensitivity to global change
486 drivers and in their seasonal dynamics – also highlighting the importance of integrating seasonal effects
487 into experimental frameworks. This may lead to far-reaching alterations of crucial ecosystem processes,
488 since decomposition and nutrient cycling are driven by the interdependent concurrence of soil microbial
489 and faunal activities (Simpson *et al.*, 2012). By covering a range of different taxonomic and trophic levels

490 of soil organisms, we could therefore show that not only interacting, but also single global change drivers

491 induce complex changes in soil food webs and functions.

492

References

Altermann, M., Rinklebe, J., Merbach, I., Körschens, M., Langer, U., Hofmann, B., 2005. Chernozem—Soil of the Year 2005. Journal of Plant Nutrition and Soil Science 168, 725-740.

Anderson, J., Domsch, K., 1978. A physiological method for the quantitative measurement of microbial biomass in soils. Soil biology and biochemistry 10, 215-221.

Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu. Rev. Plant Biol. 57, 233-266.

Baldrian, P., Merhautová, V., Petránková, M., Cajthaml, T., Šnajdr, J., 2010. Distribution of microbial biomass and activity of extracellular enzymes in a hardwood forest soil reflect soil moisture content. Applied Soil Ecology 46, 177-182.

Barton, K., 2018. Package 'MuMIn'. R package version 1.40. 4.

Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. Oecologia 165, 553-565.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological applications 20, 30-59.

Bongers, T., 1988. The nematodes of the Netherlands. The nematodes of the Netherlands.

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. Applied Soil Ecology 10, 239-251.

Borer, E.T., Harpole, W.S., Adler, P.B., Lind, E.M., Orrock, J.L., Seabloom, E.W., Smith, M.D., 2014. Finding generality in ecology: a model for globally distributed experiments. Methods in Ecology and Evolution 5, 65-73.

Briones, M., Bol, R., Sleep, D., Allen, D., Sampedro, L., 2001. Spatio-temporal variation of stable isotope ratios in earthworms under grassland and maize cropping systems. Soil Biology and Biochemistry 33, 1673-1682.

Briones, M.J.I., Ineson, P., Piearce, T.G., 1997. Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. Applied Soil Ecology 6, 117-134.

Campbell, B.J., Polson, S.W., Hanson, T.E., Mack, M.C., Schuur, E.A., 2010. The effect of nutrient deposition on bacterial communities in Arctic tundra soil. Environmental microbiology 12, 1842-1854.

Carrillo, Y., Ball, B.A., Strickland, M.S., Bradford, M.A., 2012. Legacies of plant litter on carbon and nitrogen dynamics and the role of the soil community. Pedobiologia 55, 185-192.

Cesarz, S., Reich, P.B., Scheu, S., Ruess, L., Schaefer, M., Eisenhauer, N., 2015. Nematode functional guilds, not trophic groups, reflect shifts in soil food webs and processes in response to interacting global change factors. Pedobiologia 58, 23-32.

Coleman, D.C., Crossley Jr, D.A., Hendrix, P.F., 2004. Fundamentals of soil ecology. Academic press.

Cornwell, W.K., Cornelissen, J.H., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters 11, 1065-1071.

Craven, D., Isbell, F., Manning, P., Connolly, J., Bruelheide, H., Ebeling, A., Roscher, C., Van Ruijven, J., Weigelt, A., Wilsey, B., 2016. Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. Phil. Trans. R. Soc. B 371, 20150277.

Cruz-Martínez, K., Suttle, K.B., Brodie, E.L., Power, M.E., Andersen, G.L., Banfield, J.F., 2009. Despite strong seasonal responses, soil microbial consortia are more resilient to long-term changes in rainfall than overlying grassland. The ISME journal 3, 738.

Cusack, D.F., Silver, W.L., Torn, M.S., Burton, S.D., Firestone, M.K., 2011. Changes in microbial community characteristics and soil organic matter with nitrogen additions in two tropical forests. Ecology 92, 621-632.

Dan, W., Qian, Y., Zhang, J.-Z., Shuang, W., Xue-Li, C., Zhang, X.-L., Wei-Qun, L., 2008. Bacterial community structure and diversity in a black soil as affected by long-term fertilization. Pedosphere 18, 582-592.

De Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setälä, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nature Climate Change 2, 276-280.

Deng, Q., Zhou, G., Liu, J., Liu, S., Duan, H., Zhang, D., 2010. Responses of soil respiration to elevated carbon dioxide and nitrogen addition in young subtropical forest ecosystems in China. Biogeosciences 7, 315-328.

Dyckmans, J., Scrimgeour, C.M., Schmidt, O., 2005. A simple and rapid method for labelling earthworms with 15N and 13C. Soil Biology and Biochemistry 37, 989-993.

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. Global Change Biology 18, 435-447.

Ferris, H., Bongers, T., De Goede, R., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied soil ecology 18, 13-29.

Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global patterns in belowground communities. Ecology letters 12, 1238-1249.

Frampton, G.K., Van Den Brink, P.J., Gould, P.J., 2000. Effects of spring drought and irrigation on farmland arthropods in southern Britain. Journal of Applied Ecology 37, 865-883.

Galantini, J., Rosell, R., 2006. Long-term fertilization effects on soil organic matter quality and dynamics under different production systems in semiarid Pampean soils. Soil and Tillage Research 87, 72-79.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320, 889-892.

Gardi, C., Montanarella, L., Arrouays, D., Bispo, A., Lemanceau, P., Jolivet, C., Mulder, C., Ranjard, L., Römbke, J., Rutgers, M., 2009. Soil biodiversity monitoring in Europe: ongoing activities and challenges. European Journal of Soil Science 60, 807-819.

Gongalsky, K.B., Persson, T., Pokarzhevskii, A.D., 2008. Effects of soil temperature and moisture on the feeding activity of soil animals as determined by the bait-lamina test. Applied Soil Ecology 39, 84-90.

Gough, L., Osenberg, C.W., Gross, K.L., Collins, S.L., 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos 89, 428-439.

Graenitz, J., Bauer, R., 2000. The effect of fertilization and crop rotation on biological activity in a 90 year long-term experiment. BODENKULTUR-WIEN AND MUNCHEN- 51, 99-106.

Griffiths, R.I., Whiteley, A.S., O'Donnell, A.G., Bailey, M.J., 2003. Physiological and community responses of established grassland bacterial populations to water stress. Applied and environmental microbiology 69, 6961-6968.

Gudleifsson, B., 2002. Impact of long term use of fertilizer on surface invertebrates in experimental plots in a permanent hayfield in Northern-Iceland. Agric. Soc. Iceland 15, 37-49.

Hamel, C., Schellenberg, M.P., Hanson, K., Wang, H., 2007. Evaluation of the “bait-lamina test” to assess soil microfauna feeding activity in mixed grassland. Applied Soil Ecology 36, 199-204.

Harris, R., 1981. Effect of water potential on microbial growth and activity. Water potential relations in soil microbiology, 23-95.

Helling, B., Pfeiff, G., Larink, O., 1998. A comparison of feeding activity of collembolan and enchytraeid in laboratory studies using the bait-lamina test. Applied Soil Ecology 7, 207-212.

Hueso, S., García, C., Hernández, T., 2012. Severe drought conditions modify the microbial community structure, size and activity in amended and unamended soils. Soil Biology and Biochemistry 50, 167-173.
IPCC, T.P.S.B., 2007, 2007. Climate Change 2007. The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. . Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
Kaneko, N., Kofuji, R.-i., 2000. Effects of soil pH gradient caused by stemflow acidification on soil microarthropod community structure in a Japanese red cedar plantation: an evaluation of ecological risk on decomposition. Journal of forest research 5, 157-162.
Kaneko, N., McLean, M., Parkinson, D., 1995. Grazing preference of Onychiurus subtenuis (Collembola) and Oppiella nova (Oribatei) for fungal species inoculated on pine needles. Pedobiologia 39, 538-546.
Kardol, P., Cregger, M.A., Campany, C.E., Classen, A.T., 2010. Soil ecosystem functioning under climate change: plant species and community effects. Ecology 91, 767-781.
Kent, A.D., Triplett, E.W., 2002. Microbial communities and their interactions in soil and rhizosphere ecosystems. Annual Reviews in Microbiology 56, 211-236.
Kratz, W., 1998. The bait-lamina test. Environmental Science and Pollution Research 5, 94-96.
Lamarque, J.F., Kiehl, J., Brasseur, G., Butler, T., Cameron-Smith, P., Collins, W., Collins, W., Granier, C., Hauglustaine, D., Hess, P., 2005. Assessing future nitrogen deposition and carbon cycle feedback using a multimodel approach: Analysis of nitrogen deposition. Journal of Geophysical Research: Atmospheres 110.
Li, J.H., Yang, Y.J., Li, B.W., Li, W.J., Wang, G., Knops, J.M., 2014. Effects of nitrogen and phosphorus fertilization on soil carbon fractions in alpine meadows on the Qinghai-Tibetan Plateau. PloS one 9, e103266.
Lindberg, N., Engtsson, J.B., Persson, T., 2002. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. Journal of Applied Ecology 39, 924-936.
Liu, E., Yan, C., Mei, X., He, W., Bing, S.H., Ding, L., Liu, Q., Liu, S., Fan, T., 2010. Long-term effect of chemical fertilizer, straw, and manure on soil chemical and biological properties in northwest China. Geoderma 158, 173-180.
Liu, L., Greaver, T.L., 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. Ecology Letters 13, 819-828.
Lüdecke, D., 2018. ggeffects: Create Tidy Data Frames of Marginal Effects for ggplot (Version 0.3.4). R software.
Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93, 930-938.
Maraldo, K., Holmstrup, M., 2010. Enchytraeids in a changing climate: a mini-review. Pedobiologia 53, 161-167.
Maraun, M., Alphei, J., Beste, P., Bonkowski, M., Buryn, R., Migge, S., Peter, M., Schaefer, M., Scheu, S., 2001. Indirect effects of carbon and nutrient amendments on the soil meso-and microfauna of a beechwood. Biology and Fertility of Soils 34, 222-229.
Marinari, S., Masciandaro, G., Ceccanti, B., Grego, S., 2000. Influence of organic and mineral fertilisers on soil biological and physical properties. Bioresource technology 72, 9-17.
Okada, H., Harada, H., Kadota, I., 2005. Fungal-feeding habits of six nematode isolates in the genus Filenchus. Soil Biology and Biochemistry 37, 1113-1120.
Oliver, M.A., Gregory, P., 2015. Soil, food security and human health: a review. European Journal of Soil Science 66, 257-276.
Orchard, V.A., Cook, F., 1983. Relationship between soil respiration and soil moisture. Soil Biology and Biochemistry 15, 447-453.

Pailler, A., Vennetier, M., Torre, F., Ripert, C., Guiral, D., 2014. Forest soil microbial functional patterns and response to a drought and warming event: Key role of climate–plant–soil interactions at a regional scale. Soil Biology and Biochemistry 70, 1-4.

Pan, Y., Cassman, N., de Hollander, M., Mendes, L.W., Korevaar, H., Geerts, R.H., van Veen, J.A., Kuramae, E.E., 2014. Impact of long-term N, P, K, and NPK fertilization on the composition and potential functions of the bacterial community in grassland soil. FEMS microbiology ecology 90, 195-205.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2017. nlme: Linear and nonlinear mixed effects models (R package version 3.1-128, 2016). R software.

R Core Team, R.C.T., 2017. R: A language and environment for statistical computing. Vienna, Austria; 2014.

Ramirez, K.S., Craine, J.M., Fierer, N., 2010. Nitrogen fertilization inhibits soil microbial respiration regardless of the form of nitrogen applied. Soil Biology and Biochemistry 42, 2336-2338.

Riutta, T., Clack, H., Crockatt, M., Slade, E.M., 2016. Landscape-scale implications of the edge effect on soil fauna activity in a temperate forest. Ecosystems 19, 534-544.

Roberson, E.B., Firestone, M.K., 1992. Relationship between desiccation and exopolysaccharide production in a soil Pseudomonas sp. Applied and Environmental Microbiology 58, 1284-1291.

Rożen, A., Sobczyk, Ł., Liszka, K., Weiner, J., 2010. Soil faunal activity as measured by the bait-lamina test in monocultures of 14 tree species in the Siemianice common-garden experiment, Poland. Applied Soil Ecology 45, 160-167.

Ruess, L., 1995. Studies on the nematode fauna of an acid forest soil: spatial distribution and extraction. Nematologica, 41 1, 229-239.

Scheu, S., 1992. Automated measurement of the respiratory response of soil microcompartments: active microbial biomass in earthworm faeces. Soil Biology and Biochemistry 24, 1113-1118.

Siepel, H., 1996. Biodiversity of soil microarthropods: the filtering of species. Biodiversity & Conservation 5, 251-260.

Simpson, J.E., Slade, E., Riutta, T., Taylor, M.E., 2012. Factors affecting soil fauna feeding activity in a fragmented lowland temperate deciduous woodland. PLOS ONE 7, e29616.

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

Song, M., Li, X., Jing, S., Lei, L., Wang, J., Wan, S., 2016. Responses of soil nematodes to water and nitrogen additions in an old-field grassland. Applied soil ecology 102, 53-60.

Sorensen, P.O., Germino, M.J., Feris, K.P., 2013. Microbial community responses to 17 years of altered precipitation are seasonally dependent and coupled to co-varying effects of water content on vegetation and soil C. Soil Biology and Biochemistry 64, 155-163.

Steffen, W., Sanderson, R.A., Tyson, P.D., Jäger, J., Matson, P.A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H.-J., Turner, B.L., 2006. Global change and the earth system: a planet under pressure. Springer Science & Business Media.

Stevens, C.J., Lind, E.M., Hautier, Y., Harpole, W.S., Borer, E.T., Hobbie, S., Seabloom, E.W., Ladwig, L., Bakker, J.D., Chu, C., 2015. Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. Ecology 96, 1459-1465.

Thakur, M.P., Reich, P.B., Hobbie, S.E., Stefanski, A., Rich, R., Rice, K.E., Eddy, W.C., Eisenhauer, N., 2018. Reduced feeding activity of soil detritivores under warmer and drier conditions. Nature Climate Change 8, 75.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102, 8245-8250.

Tonkin, J.D., Bogan, M.T., Bonada, N., Rios-Touma, B., Lytle, D.A., 2017. Seasonality and predictability shape temporal species diversity. Ecology 98, 1201-1216.

Treseder, K.K., 2008. Nitrogen additions and microbial biomass: A meta-analysis of ecosystem studies. Ecology Letters 11, 1111-1120.

Van der Wal, A., Geerts, R., Korevaar, H., Schouten, A., op Akkerhuis, G.J., Rutgers, M., Mulder, C., 2009. Dissimilar response of plant and soil biota communities to long-term nutrient addition in grasslands. Biology and fertility of soils 45, 663-667.

Vitousek, P.M., 1994. Beyond global warming: ecology and global change. Ecology 75, 1861-1876.

Vogel, A., Fester, T., Eisenhauer, N., Scherer-Lorenzen, M., Schmid, B., Weisser, W.W., Weigelt, A., 2013. Separating drought effects from roof artifacts on ecosystem processes in a grassland drought experiment. PloS one 8, e70997.

Waldrop, M., Firestone, M., 2006. Seasonal dynamics of microbial community composition and function in oak canopy and open grassland soils. Microbial Ecology 52, 470-479.

Wall, D.H., Nielsen, U.N., Six, J., 2015. Soil biodiversity and human health. Nature.

Wan, S., Norby, R.J., Ledford, J., Weltzin, J.F., 2007. Responses of soil respiration to elevated CO2, air warming, and changing soil water availability in a model old-field grassland. Global Change Biology 13, 2411-2424.

Wang, R., Balkanski, Y., Boucher, O., Ciais, P., Peñuelas, J., Tao, S., 2015a. Significant contribution of combustion-related emissions to the atmospheric phosphorus budget. Nature Geoscience 8, 48.

Wang, S., Tan, Y., Fan, H., Ruan, H., Zheng, A., 2015b. Responses of soil microarthropods to inorganic and organic fertilizers in a poplar plantation in a coastal area of eastern China. Applied Soil Ecology 89, 69-75.

Wardle, D., Yeates, G., 1993. The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer food-webs. Oecologia 93, 303-306.

Wever, L.A., Lysyk, T.J., Clapperton, M.J., 2001. The influence of soil moisture and temperature on the survival, aestivation, growth and development of juvenile Aporrectodea tuberculata (Eisen)(Lumbricidae). Pedobiologia 45, 121-133.

Yahdjian, L., Sala, O.E., 2002. A rainout shelter design for intercepting different amounts of rainfall. Oecologia 133, 95-101.

Yeates, G., Bongers, T., De Goede, R., Freckman, D., Georgieva, S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. Journal of nematology 25, 315.

Zhou, L., Zhou, X., Shao, J., Nie, Y., He, Y., Jiang, L., Wu, Z., Hosseini Bai, S., 2016. Interactive effects of global change factors on soil respiration and its components: a meta-analysis. Global change biology 22, 3157-3169.