



Climate change and land use induce functional shifts in soil nematode communities

Julia Siebert^{1,2} · Marcel Ciobanu³ · Martin Schädler^{1,4} · Nico Eisenhauer^{1,2}

Received: 14 January 2019 / Accepted: 12 November 2019 / Published online: 28 November 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Land-use intensification represents one major threat to the diversity and functioning of terrestrial ecosystems. In the face of concurrent climate change, concerns are growing about the ability of intensively managed agroecosystems to ensure stable food provisioning, as they may be particularly vulnerable to climate extreme-induced harvest losses and pest outbreaks. Extensively managed systems, in contrast, were shown to mitigate climate change based on plant diversity-mediated effects, such as higher functional redundancy or asynchrony of species. In this context, the maintenance of soils is essential to sustain key ecosystem functions such as nutrient cycling, pest control, and crop yield. Within the highly diverse soil fauna, nematodes represent an important group as their trophic spectrum ranges from detritivores to predators and they allow inferences to the overall state of the ecosystem (bioindicators). Here, we investigated the effects of simulated climate change and land-use intensity on the diversity and abundance of soil nematode functional groups and functional indices in two consecutive years. We revealed that especially land use induced complex shifts in the nematode community with strong seasonal dynamics, while future climate led to weaker effects. Strikingly, the high nematode densities associated with altered climatic conditions and intensive land use were a consequence of increased densities of opportunists and potential pest species (i.e., plant feeders). This coincided with a less diverse and less structured community with presumably reduced capabilities to withstand environmental stress. These degraded soil food web conditions represent a potential threat to ecosystem functioning and underline the importance of management practices that preserve belowground organisms.

Keywords Global change · Food-web complexity · Food security · Agroecosystem management · Belowground diversity

Communicated by Liliane Ruess.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-019-04560-4>) contains supplementary material, which is available to authorized users.

✉ Julia Siebert
julia.siebert@idiv.de

- 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 Institute of Biological Research, Branch of the National Institute of Research and Development for Biological Sciences, 48 Republicii Street, 400015 Cluj-Napoca, Romania
- ⁴ Department of Community Ecology, Helmholtz-Centre for Environmental Research – UFZ, Theodor-Lieser-Str. 4, 06120 Halle, Germany

Introduction

Confronted with a world population growing at unprecedented pace, humankind strives to optimize agricultural practices to maximize yields (Smith et al. 2016). Following this increasing demand for food provisioning to humans and livestock as well as for natural resources in general, we can observe as a global trend that tracts of land are progressively converted into agriculturally managed systems that are dedicated to optimized production (Foley et al. 2005; Smith et al. 2016; Wheeler and Von Braun 2013). Thus, land-use intensification has long been identified as one of the major global change drivers, severely impacting terrestrial ecosystems worldwide (Maxwell et al. 2016; Newbold et al. 2015; Sala et al. 2000; Tilman et al. 2002). Such intensification processes include, for instance, a selection of high-yielding crop varieties and the restriction to a few top-performing forage species, the employment of heavy machinery for rigorous tillage, and short mowing intervals (Giller et al.

1997; Newbold et al. 2015; Tilman et al. 2002; Tsiafouli et al. 2015; Yagioka et al. 2015). This often implies a high use of mineral fertilizers and pesticides that further impair the integrity of such managed ecosystems (Marinari et al. 2000; Ramirez et al. 2010; Treseder 2008).

A growing body of literature questions the capability of these intensified systems to ensure food security in the long term, as they might be particularly susceptible to harvest losses due to climate extremes (Isbell et al. 2017; Lobell et al. 2008). Notably, such climate extremes are likely to become more frequent in Central Europe in the future, and climate change includes general warming trends of soil and air temperatures as well as altered seasonal precipitation patterns leading to extended drought periods over summer, whereas spring and fall may receive considerably more rainfall (Doscher et al. 2002; IPCC 2007; Jacob and Podzun 1997; Kerr 2007; Meinke et al. 2010). Given that the strength of climate change effects may be mediated by land use (De Vries et al. 2012), this puts additional pressure on intensively managed, often low-diversity systems that might lack the ability to buffer or to recover after such disturbances in a reasonable timeframe (Lobell et al. 2008; Yachi and Loreau 1999). In this context, extensive management practices—both in grasslands as well as in farming systems—were identified as one promising avenue to mitigate detrimental climate change effects (De Vries et al. 2012; Isbell et al. 2017). Such extensive management practices largely refrain from using pesticides and/or mineral fertilizer, often representing more diverse mixtures or following specific crop rotation cycles that include green manuring (legumes) in every third year of the cycle. While extensive systems may lead to lower yields or slower pest control, their great benefits in the context of climate extremes are based on the fact that they include less disturbances and allow more complex and thus more diverse systems with a plethora of survival and coping strategies (e.g., functional redundancy or asynchrony) (Díaz and Cabido 2001; Mazancourt et al. 2013) maintaining a multitude of ecosystem functions (Birkhofer et al. 2011; Goldenberg et al. 2018; Hautier et al. 2015; Isbell et al. 2015, 2017; Scialabba and Müller-Lindenlauf 2010).

The maintenance of the productivity and fertility of soils represents a key aspect of less-intensive and sustainable management of agricultural fields (Tilman et al. 2002). Soils harbor a significant portion of terrestrial biodiversity and are crucial for many ecosystem functions like nutrient cycling, crop yields, and pest control (Bardgett and van der Putten 2014; Brussaard et al. 2007; Wall et al. 2015). At the same time, soil biota are known to be highly susceptible to intensive agricultural management, thus putting their associated services at risk (Bengtsson et al. 2005; Culman et al. 2010; Tsiafouli et al. 2015). In addition, indirect effects on soil biota via changes in water-use efficiency,

erosion, and overall soil quality were reported (Dendooven et al. 2012). Notably, land-use effects could also change the entire structure of soil food webs, e.g. by strongly decreasing the abundances of predators, which are known to be more vulnerable to disturbances than lower trophic levels (Murrell and Barton 2017; Voigt et al. 2007). As a consequence, predator–prey interactions that are crucial for biological pest control might be disrupted, subsequently impacting plant growth and crop yields. Organic farming was also shown to sustain high evenness of predators, hereby reducing the risk of pest outbreaks (Crowder et al. 2010; Murrell and Barton 2017; Wilby and Thomas 2002). Concurring climate change may superimpose such negative effects of intensive management on soil organisms with thus far widely unknown consequences.

Amongst the different groups of soil organisms, free-living nematodes occur in exceptionally high numbers and represent one of the most diverse metazoan groups in terrestrial ecosystems (Bernard 1992). They have a special position within the soil fauna for several reasons: first, they cover all major trophic groups of the soil food web ranging from detritivores to herbivores and predators (Ferris 2010; Yeates et al. 1993), which makes them particularly suitable for studying global change effects on different trophic levels within the same faunistic group. Second, they are useful bioindicators with their functional shifts providing valuable information on the state of an ecosystem, and thus allowing inferences to other biotic groups and soil health (Ferris et al. 2001). Third, herbivorous nematodes are known as important agricultural pests (Evans et al. 1993), making knowledge about their performance under different land-use and climate scenarios highly relevant for farmers. While nematodes are often comparatively unaffected by climate warming (Cesarz et al. 2015; De Long et al. 2016; Yeates et al. 2002), different land-use practices were shown to strongly impact nematode functional groups and thus nematode community structure (Postma-Blaauw et al. 2010; Tsiafouli et al. 2015; Yeates et al. 1999). As nematodes cover a wide range of life-history and feeding strategies, the different functional groups show vastly different responses to environmental disturbances and global change: while opportunistic nematodes, that are known as typical *r*-strategists or colonizers, might be able to benefit from enhanced plant growth and higher nutrient availability under land-use intensification, the more sensitive nematode groups consisting of *K*-strategists (i.e., persisters) may decline, resulting in simplified and less structured soil food webs (Ferris et al. 2001). Such shifts can be captured by nematode functional indices that allow drawing general conclusions about the state of the ecosystem (Bongers 1990). Our current knowledge of how interactive global change drivers (e.g., climate change and land use) affect soil nematode communities in managed agricultural systems remains scarce though.

Here, we investigate the effects of climate change in different land-use scenarios (managed grasslands and farmlands) on the diversity and abundance of free-living soil nematode functional groups and nematode functional indices. The study was conducted within the Global Change Experimental Facility (GCEF) in Bad Lauchstädt, Germany. With this large-scale experimental platform, climatic conditions predicted for the region for ~2070–2100 (referred hereafter as ‘future climate’) are simulated by altered temperature (ambient versus ambient +0.6 °C) and precipitation regimes (ambient versus ~20% reduction in summer, ~10% addition in spring and fall, respectively) using fully automated fold-out roofs (Schädler et al. 2019). The manipulations reflect realistic scenarios that allow for inter-annual variability instead of highly controlled conditions. The climate treatments are crossed with five different land-use scenarios in a split-plot design (Fig. S1a) that all represent common local management practices (including a specific plant species pool, crop rotations, and management strategies/intervals). By covering two highly relevant seasons for soil processes in two consecutive years (spring and fall in 2015 and 2016), we were able to obtain a comprehensive picture of soil nematode responses to interacting global change drivers across seasons.

We hypothesized that (1) soil nematode diversity will be lowest at high levels of land-use intensity (i.e., in conventional farmlands and intensively used grasslands). Furthermore, (2) climate change effects on soil nematode communities will be most pronounced on those intensively managed land-use types, whereas the organic farmland and the two extensive grasslands might be able to buffer the detrimental effects of future climatic conditions due to a more sustainable, soil-protecting crop rotation in the case of the farmland and higher biodiversity in case of the grasslands. (3) Furthermore, we expected different responses within the nematode fauna to interacting global change drivers. While opportunistic nematodes might benefit from increased resource availability under intensive management (i.e., fertilization, high plant biomass) and ambient conditions, higher trophic groups in particular may decline under intensive management and future climatic conditions, thus leading to simplified, less structured communities.

Methods

Study design

The study site is located at the field research station of the Helmholtz-Centre for Environmental Research (UFZ) in Bad Lauchstädt, Germany (51° 22′ 60 N, 11° 50′ 60 E, 118 m a.s.l.), and was formerly used as an arable field (last crop cultivation in 2012). The site is located in the Central

German dry area (Querfurter Platte) and characterized by a mean annual temperature of 8.9 °C (1896–2013) and a mean annual precipitation of 489 mm (1896–2013). The soil is a Haplic Chernozem with a humus layer reaching down to more than 40 cm depth. This highly fertile soil type was developed upon carbonatic loess substrates (around 70% silt and 20% clay content). The soil is known for its high water-retention capacity (nearly reaching the mean annual precipitation), ensuring comparatively low susceptibility to drought stress (Altermann et al. 2005). Within the upper 15 cm, pH values ranged from 5.8 to 7.5, total carbon and total nitrogen content varied between 1.71–2.09% and 0.15–0.18%, respectively.

The Global Change Experimental Facility was established in 2013 to study the interactive effects of climate change (including elevated temperature and changes in precipitation patterns) and land-use intensity on managed terrestrial ecosystems using realistic scenarios. Each land-use scenario represents a common local management type (rather than an experimental gradient) that entails several facets like plant diversity and community structure, management intervals, crop rotation, and fertilization, for which the responses to climate change can be assessed (see Table S1 for an overview of the land-use history of the site). The climate treatments were first applied in 2014 (spring 2014: start of temperature treatment; summer 2014: start of precipitation treatment). The experiment consists of 50 plots arranged in ten mainplots (Fig. S1a). The two experimental treatments are implemented in a split-plot design with the climate treatment carried out at the mainplot level ($n = 10$) and the land-use treatment implemented at the plot level ($n = 50$), randomly arranged within the mainplots. This results in five replicates of each combined experimental treatment (climate x land use). Thus, for each land-use type there are five plots with future climatic conditions and five plots with ambient climatic conditions that serve as a climate control. A relevant spatial scale is realized by a large plot size of 16 × 24 m that allows to employ equipment commonly used in the agricultural sector. Each plot has a buffer zone of 2 m to the eastern and western sides and 4.5 m to the southern and northern sides. Soil sampling took place in the inner plot area (15 × 12 m) on a specific transect for soil measurements (Fig. S1b). Five of the mainplots have ambient climatic conditions with steel constructions (5 m height) to control for potential infrastructure effects, such as microclimatic effects. The other five mainplots represent future climatic conditions, which means that their roof constructions include an irrigation system and mobile roof and side panels that can be closed via rain sensors and timers. The climate treatments were chosen based on a consensus scenario across several dynamic models for Central Germany for 2070–2100 [COSMO-CLM (Rockel et al. 2008), REMO (Jacob and Podzun 1997), and RCAO (Doscher et al.

2002)], which include higher inter-annual rainfall variability with longer drought periods over summer and increased precipitation in spring and fall. Furthermore, the mean annual temperature is predicted to rise up to 3 °C. The treatments are applied as realistic climate scenarios, which include natural variability instead of highly controlled conditions. Thus, the climate treatments are applied relative to the ambient conditions and allow for inter-annual variability. Over summer (June–August), the climate treatment includes a reduction of precipitation by 20% (closing of roof and side panels via rain sensors). In spring (March–May) and fall (September–November), the precipitation is increased by 10% by the use of an irrigation system that uses water from a large rain water reservoir (Fig. S2). Passive warming overnight, which increases air and soil temperature on average by ~0.6 °C, is realized during the active roofing phase (Table S2). In 2015, the roofing phase started on February 25th and ended on December 11th (roofs were closed 79% of night time, deviations were due to frost and wind). In 2016, the roofing phase started on March 23rd and ended on November 23rd (roofs were closed 82% of night time).

Within each mainplot, the five plots represent the five different land-use treatments, with different levels of land-use intensity: (1) conventional farmland; (2) organic farmland; (3) intensively mown grassland; (4) extensively mown grassland; and (5) extensively grazed grassland. The conventional and organic farmlands are managed according to commonly used management practices in the region. For the conventional farmland, this includes a crop rotation consisting of winter rape, winter wheat, and winter barley. Mineral fertilization as well as herbicides, fungicides, and insecticides are applied at realistic rates and frequencies. The organic farmland has significantly stricter regulations concerning fertilization (only allowing legumes for nitrogen fixation in every third year, and the application of rock phosphate (P–Ca–Mg) and patent kali (K–Mg–S) in the first year of the crop cycle) and pesticides (mainly mechanical weed control using harrows). A bipartite crop sequence is applied, in which alfalfa and white clover are intended to be planted in the first and fourth year of the cycle. The other crop cycles also include winter wheat and winter barley as on the conventional farmland. In addition, the three grasslands represent common management types in the region. The intensively managed grassland consists of typical forage species and is fertilized with mineral fertilizer and frequently mown (three times in 2015, four times in 2016), whereas the extensively managed grasslands are either moderately mown (twice in 2015 and 2016, no fertilization) or moderately grazed by sheep (twice in 2015, three times in 2016, by a group of 20 sheep grazing on each plot for 24 h). After each mowing event, the plant biomass is removed from the plots, as it would normally happen during hay harvest. On the extensively mown grassland, the mown biomass was left

on the plots for some days to allow natural sowing. While the extensively used grasslands contain 53.1 ± 2.0 plant species per 9 m^2 , the intensively used grassland has 10.1 ± 3.6 plant species per 9 m^2 (mean \pm SD for 2015–2017). For details on the plant species pools, see Data S1 in the supplementary information.

Nematode sampling and analyses

Soil samples were taken on a transect within the inner plot area in May and October 2015 and 2016 using a steel corer (1 cm diameter; 15 cm deep). Seven subsamples per plot were homogenized, sieved at 2 mm, and stored at 4 °C. 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 gauze (200 μm) at the bottom and placed in water-filled funnels. More water was added to saturate the soil samples 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 gauze 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 a 4% formaldehyde solution. All nematodes per sample were counted at 100 \times magnification using a Leica DMI 4000B light microscope. Identification was conducted at 400 \times magnification. For identification, sediment material from the bottom of each sample vial was extracted with a 2 ml plastic pipette and examined in temporary-mounted microscope slides. At least 100 well-preserved specimens (if available in the sample) were randomly selected and identified to genus (adults and most of the juveniles) or family level (juveniles), following Bongers (1988). Nematode taxa were then arranged into trophic groups (bacteria, fungal, and plant feeders, omnivores, and predators) (Okada et al. 2005; Yeates et al. 1993). Due to low densities, omnivorous and predatory nematodes were grouped into a combined feeding type for most analyses (but see Figs. S3–4 and Table S3 for treatment effects on individual groups). This is justified by the fact that both groups often respond similar to environmental disturbances, as they mainly consist of *K*-strategists and represent higher trophic levels (Bongers and Ferris 1999; Porazinska et al. 2003). In addition, the ratio between microbivores (bacteria feeders and fungal feeders) and plant feeders was calculated to evaluate the net effect of the nematode community on plant productivity. Ratios above 1.0 indicate that beneficial effects are stronger than negative effects (Eisenhauer et al. 2011; Wasilewska 1997). Nematodes were ordered according to the colonization-persistence gradient (*c*–*p* values) (Bongers 1990; Bongers and Bongers 1998) based on their life-history strategy (i.e., *r*- or *K*-strategists). Nematodes included in the

cp-1 category are characterized by their short generation cycles and high fecundity. They mainly feed on bacteria. Nematodes assigned to the cp-2 class have longer generation times, lower fecundity, and consist of bacterivores and fungivores (Ferris et al. 2001). Both cp-1 and cp-2 groups are categorized as *r*-strategists. Nematodes belonging to cp-3 to cp-5 classes are *K*-strategist with longer generation times, higher trophic feeding levels and increasing sensitivity against disturbances (Ferris et al. 2001). The *c*–*p* scaling was used to calculate the Maturity Index (MI) of nematode communities according to the following formula:

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

where $v(i)$ is the *c*–*p* value of taxon *i* and $f(i)$ is the frequency of that taxon in a sample. MI is used to assess environmental disturbance, soil health, and as an indicator of overall soil food-web complexity (Bongers 1990; Bongers and Bongers 1998). Furthermore, nematode taxa were assigned to functional guilds according to Ferris et al. (2001), which then served as a basis to calculate the Enrichment Index, Channel Index, and Structure Index to assess ecosystem functions. Functional guilds refer to the following trophic groups: bacterial feeders (Ba_x), fungal feeders (Fu_x), omnivores (Om_x), and carnivores (Ca_x). The associated numbers (i.e., the *x* of the respective trophic group) refer to the *c*–*p* values mentioned above. The Enrichment Index (EI) indicates the responsiveness of the opportunistic bacteria (Ba_1 and Ba_2) and fungal feeders (Fu_2) to food-web enrichment (Ferris et al. 2001) and is calculated as follows:

$$EI = 100 \times \left[\frac{e}{e + b} \right],$$

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

$$CI = 100 \times \left[0.8 \times \frac{Fu_2}{3.2 \times Ba_1 + 0.8 \times Fu_2} \right],$$

where 0.8 and 3.2 represent the enrichment weightings for Fu_2 and Ba_1 nematodes (Ferris et al. 2001). The Structure Index (SI) provides information about the complexity of the soil food web. High values indicate structured soil food webs with higher interconnectance between multiple trophic levels, implying ecosystem stability, while low values indicate

simplified soil food web and reflect environmental disturbance (Ferris et al. 2001):

$$SI = 100 \times \left[\frac{s}{s + b} \right],$$

where s is 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 b represents the weighted frequencies of Ba_2 and Fu_2 nematodes (Ferris et al. 2001).

In addition, nematode taxon richness, Shannon diversity index, and Pielou's evenness (referred hereafter as taxon richness, Shannon diversity and evenness) were calculated using the R package "vegan" (Oksanen et al. 2013).

Statistical analysis

Generalized mixed-effects models (GLMMs) were used to analyze the effects of climate, land use, season (spring and fall 2015 and 2016), and their interactions on nematode density (i.e., total number of nematode individuals in the community), taxon richness, and trophic groups (i.e., percentage of individuals in each trophic group). Taxon richness and density were modelled with Poisson distribution (link="log"), while the trophic groups were modelled with binomial distribution (link="logit"). Linear mixed-effects models (LMMs) were used to assess the effects of climate, land use, season (spring and fall 2015 and 2016), and their interactions on Shannon diversity, evenness, Enrichment Index, Structure Index, Channel Index, Maturity Index, and the ratio between microbivores and plant feeders. The random intercept of all models was structured with plots nested within mainplots, nested within year (year as a categorical factor). Model assumptions of both LMMs and GLMMs were checked by visually inspecting the residual plots for homogeneity and the quantile–quantile plots for normality. There was no correlation between the residuals and the fitted parameters of the model. To meet the assumptions of the model, the microbivore–plant feeder ratio had to be log transformed. GLMMs were also used to assess the effects of climate, land use, and their interactions on nematode functional guilds and *c*–*p* groups (Table S3) using binomial distribution (link="logit"). The random intercept of the model was structured with plots nested within mainplots, nested within season, nested within year (year as a categorical factor). LMMs and GLMMs were performed using the "lme4" package (Bates et al. 2014). All statistical analyses were conducted using R version 3.4.2 (R Core Team 2017).

Results

Total nematode density and taxonomic diversity metrics

Overall, the total density of nematodes was significantly increased under future climatic conditions (+16.8%; $p < 0.05$) and varied significantly across land-use types (CF = 18.85 ± 1.17 ind/g DW soil (all values are presented \pm SE), EP = 9.86 ± 0.51 ind/g DW soil; $p < 0.001$; Fig. 1a; Table 1, see Table S4 for an overview of the mean values for each response variable). According to a significant interaction of land use and season ($p < 0.001$), we found in spring that highest nematode densities were reached in conventional farmlands (19.19 ± 1.73 ind/g DW soil) and lowest densities in both extensively

used grassland treatments (EM = 9.74 ± 0.88 ind/g DW soil; EP = 9.77 ± 0.76 ind/g DW soil). In fall, the extensive grasslands still showed the lowest densities (EM = 10.60 ± 0.68 ind/g DW soil; EP = 9.95 ± 0.72 ind/g DW soil), but densities in the intensively used grasslands (23.17 ± 2.58 ind/g DW soil) exceeded those in conventional farmlands (18.51 ± 1.60 ind/g DW soil). Furthermore, nematode density was significantly affected by the interaction of climate and season ($p < 0.05$): while future climate increased densities in both seasons, the strongest effects were detected in fall (+7.3% in spring; +26.0% in fall). The lowest densities were found in spring under ambient climatic conditions (12.82 ± 0.86 ind/g DW soil).

Taxon richness was significantly affected by seasonal changes with overall lower levels in fall (−9.6%; $p < 0.01$; Fig. 1b). In addition, land use significantly influenced nematode richness ($p < 0.01$): the highest numbers of

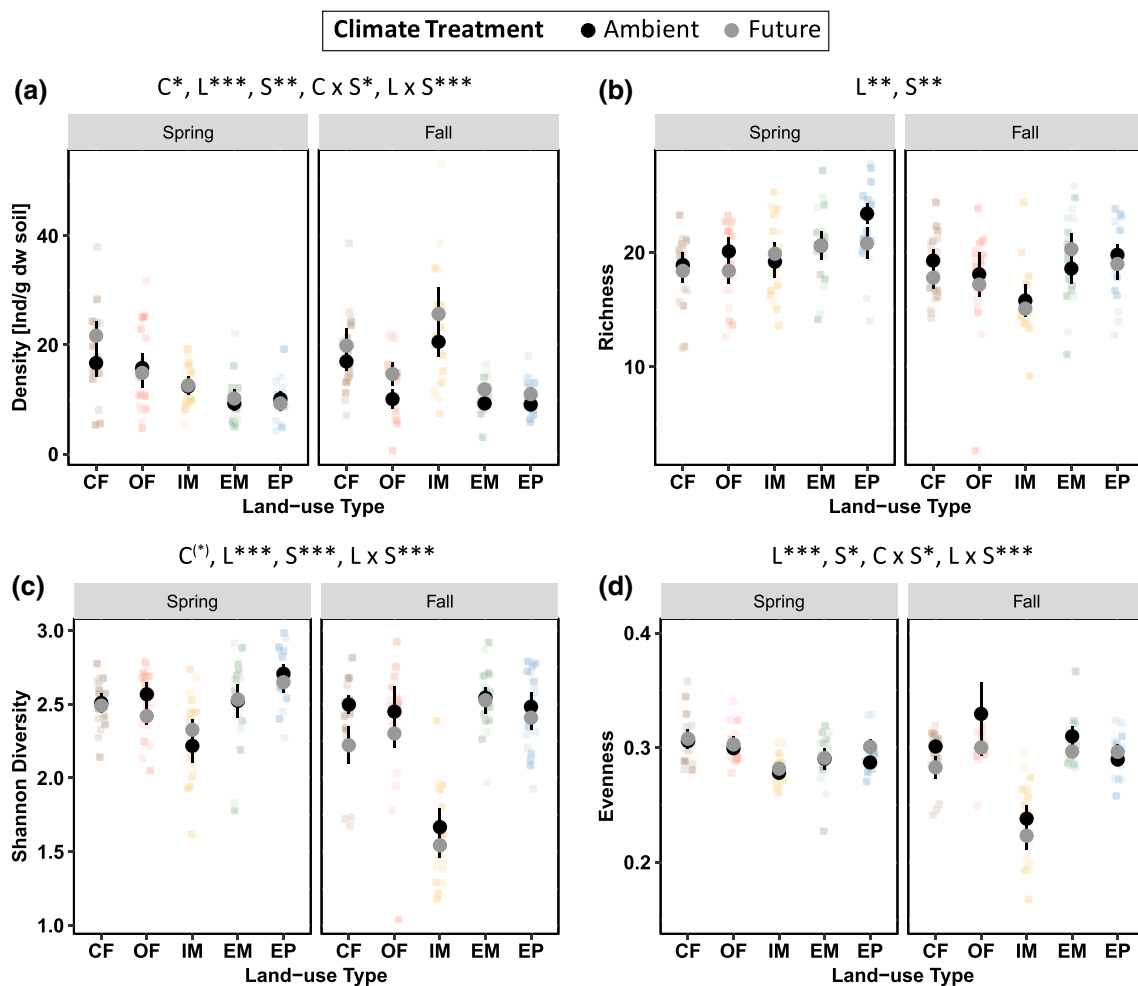


Fig. 1 Effects of climate (C), land use (L), and season (S) on nematode density and taxonomic diversity metrics **a** total nematode density per g dry weight soil; **b** nematode taxon richness; **c** Shannon diversity; and **d** evenness. Error bars represent \pm standard error. Black = ambient climate; grey = future climate. CF = conventional

farming (brown); OF = organic farming (red); IM = intensively used meadow (yellow); EM = extensively used meadow (green); EP = extensively used pasture (blue). Data from spring (May) and fall (October) 2015 and 2016 is included. (* $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (colour figure online)

Table 1 Chi-squared values (χ^2) of the generalized mixed-effects models for the effects of climate, land use, season (spring and fall 2015 and 2016), and their interaction on soil nematode variables

Nematode response variable	Climate	Land use	Season	Climate × land use	Climate × season	Land use × season	Climate × land use × season
	χ^2	χ^2	χ^2	χ^2	χ^2	χ^2	χ^2
Total density	5.22*	76.40***	8.35**	0.79	4.83*	61.04***	6.20
Taxon richness	1.04	14.02**	9.70**	2.17	0.07	5.41	1.10
Shannon diversity	3.70 ^(*)	137.09***	35.36***	2.71	1.91	35.89***	2.15
Evenness	1.30	82.27***	4.31*	3.76	6.14*	38.86***	1.28
Enrichment Index	0.39	6.02	56.09***	9.71 ^(*)	0.00	6.46	4.43
Structure Index	3.59 ^(*)	91.97***	1.77	5.27	0.00	8.82 ^(*)	7.63
Channel Index	3.78 ^(*)	6.71	23.20***	7.81	0.19	4.31	3.96
Maturity Index	0.37	52.55***	4.48*	2.54	0.00	5.21	5.47
Bacteria feeders	1.10	82.62***	23.65***	1.45	8.87**	98.06***	5.83
Fungal feeders	5.10*	169.18***	2.82 ^(*)	0.74	3.68 ^(*)	70.05***	51.66***
Plant feeders	0.10	219.88***	176.65***	4.73	0.00	106.53***	22.12***
Predators and omnivores	1.09	17.82**	0.09	3.45	0.69	22.86***	5.17
Microbivores/plant feeders (log-scaled)	0.53	223.51***	23.22***	3.16	0.06	22.83***	6.33

Poisson distribution was used to model nematode density and taxon richness; binomial distribution was used to model the percentages of each nematode trophic group. Linear mixed-effects models were used for Shannon diversity, evenness, nematode indices and ratios. Plots nested within mainplots nested within years served as a random intercept in the model

(*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

nematode taxa were found in extensively grazed grasslands (20.75 ± 0.57 taxa on average), whereas richness was particularly low in intensively used grasslands (18.45 ± 0.62 taxa on average). For Shannon diversity and evenness (Fig. 1c, d), we found a significant interaction between land use and season (Shannon diversity H' : $p < 0.001$; Evenness J' : $p < 0.001$). They were both particularly low in intensively used grasslands, with land-use effects being most pronounced in fall ($H' = 1.61 \pm 0.07$; $J' = 0.23 \pm 0.008$). The highest Shannon diversity values were reached in extensively grazed plots in spring ($H' = 2.68 \pm 0.04$), whereas greatest evenness was found in organic farmlands in fall ($J' = 0.31 \pm 0.014$). In addition, climate and season interactively affected evenness ($p < 0.05$) by showing the lowest evenness scores under future climate particularly in fall (-4.7% , $J' = 0.28 \pm 0.005$), whereas climate effects were minimal to slightly positive in spring ($+1.6\%$).

Nematode functional diversity metrics

The Enrichment Index significantly varied between seasons with higher enrichment in fall ($+23.5\%$; $p < 0.001$; Fig. 2a). The Structure Index was significantly affected by the land-use types ($p < 0.001$), clearly separating farmlands (low structure; CF = 15.35 ± 1.91 and OF = 19.75 ± 2.33) and grasslands (high structure; EM = 40.72 ± 2.94 , EP = 39.99 ± 2.66 , and IM = 48.34 ± 3.29) into two groups (Fig. 2b). The same patterns were also reflected by the

Maturity Index ($p < 0.001$), which was substantially lower in farmlands (CF = 2.00 ± 0.02 ; OF = 1.99 ± 0.02) than in grasslands (EM = 2.23 ± 0.05 ; EP = 2.21 ± 0.03 ; IM = 2.29 ± 0.04). In addition, the Maturity Index was significantly lower in fall (-2.6% ; $p < 0.05$; Fig. 2c). The Channel Index was strongly driven by seasonal patterns ($p < 0.001$) that indicate fungal-dominated decomposition pathways in spring ($+26.9\%$, high values), whereas bacteria-driven decomposition pathways were more dominant in fall (low values; Fig. 2d).

Nematode trophic groups

Bacteria-feeding nematodes were significantly affected by an interaction between land use and season ($p < 0.001$). They showed the highest densities in conventional (CF = 33.2% bacterial feeders) and organic farming plots (OF = 33.1% bacterial feeders) in spring, with particularly low levels in intensively used meadow plots in fall (IM = 10.1% bacterial feeders). Climate and season also interactively affected bacteria-feeding nematodes ($p < 0.01$): future climate had negative impacts in fall (-5.9%), but negligible effects in spring (-0.4% ; Fig. 3a). The abundances of fungal-feeding nematodes were driven by a three-way interaction between climate, land use, and season ($p < 0.001$). They were most abundant in conventional and organic farming plots under future climatic conditions in fall (CF = 42.4% fungal feeders; OF = 42.6% fungal feeders), whereas the intensively used meadow plots had the lowest abundances under future

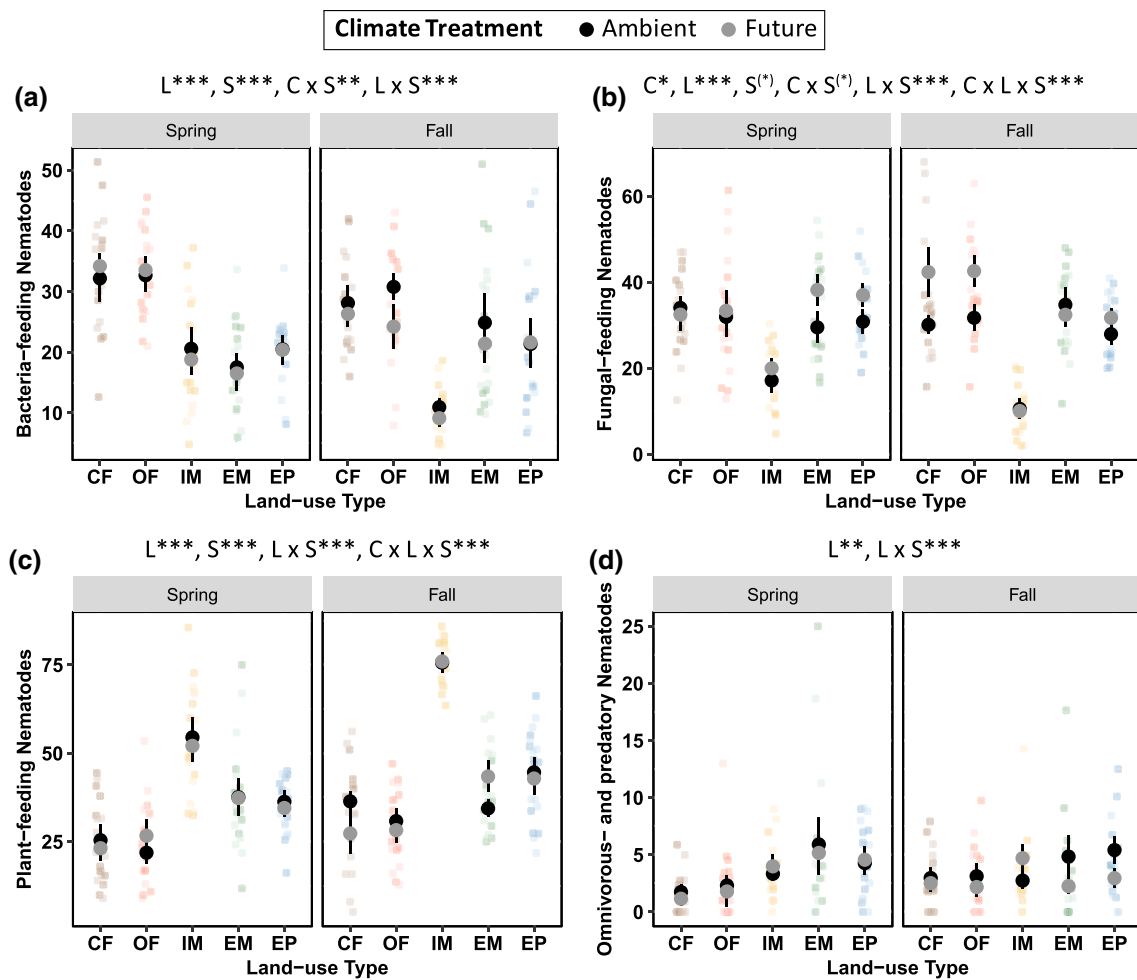


Fig. 3 Effects of climate (C), land use (L), and season (S) on nematode trophic groups **a** bacteria-feeding nematodes; **b** fungal-feeding nematodes; **c** plant-feeding nematodes; and **d** omnivorous and predatory nematodes. Error bars represent \pm standard error. Black = ambient climate; grey = future climate CF = conventional farming (brown);

OF = organic farming (red); IM = intensively used meadow (yellow); EM = extensively used meadow (green); EP = extensively used pasture (blue). Data from spring (May) and fall (October) 2015 and 2016 is included. (*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (colour figure online)

climate in fall (IM = 10.1% fungal feeders). The positive effects of future climate were most pronounced in extensively mown grasslands in spring (EM: +30.0%) and in conventional and organic farming plots in fall (CF: +37.3%; OF: +71.0%; Fig. 3b). In addition, plant-feeding nematodes were affected by a significant three-way interaction between climate, land use, and season ($p < 0.001$). They were most abundant in intensively used grassland plots in both seasons with particularly high levels in fall (future climate: IM = 76.0% plant feeders, ambient climate: IM = 75.7% plant feeders). The lowest abundances were reached on organic farmlands in spring under ambient climate (OF = 21.9% plant feeders), and the strongest negative climate effects were found on conventional farming plots in fall (−33.3%). However, future climate had a comparatively strong positive effect on plant-feeding nematodes in organic farmlands in spring (+31.3%) and in extensively mown grassland plots

in fall (+51.2%; Fig. 3c). Omnivorous and predatory nematodes were affected by the interaction between land use and season ($p < 0.001$). They generally had very low abundances, being particularly rare in conventional farming plots in spring (CF = 1.5% omnivores and predators). The highest levels were reached in grassland plots, particularly in intensively mown grasslands in spring (EM = 5.5% omnivores and predators; Fig. 3d).

The ratio between microbivores (bacteria- and fungal-feeding nematodes) and plant-feeding nematodes was significantly influenced by the interactive effects of land use and season ($p < 0.001$). Highest levels were reached in conventional farmlands in spring ($CF = 3.67 \pm 0.54$) compared to particularly low values in intensively managed grasslands in fall ($IM = 0.28 \pm 0.03$). Only the intensively managed grasslands were found below the critical value of 1.0 in both seasons, indicating overall negative soil effects on

plant productivity. For all other land-use types, values were above 1.0, and thus beneficial soil effects on plants can be assumed (Fig. 2e).

Discussion

We studied the responses of the ecologically important group of soil nematodes in two highly relevant seasons for soil processes in two consecutive years, which allowed us to obtain a comprehensive picture of their structural and functional shifts in response to interacting global change drivers across seasons. Our study revealed that especially land-use induced complex shifts in soil nematode communities with strong seasonal dynamics. The climate treatment as well as the interaction between climate and land use exerted weaker effects, but were also dependent on the season. Notably, we could show that higher nematode densities under the combination of future climate and intensive land use were realized at the expense of higher shares of opportunists and potential pest species (plant-feeding nematodes), which coincided with a less diverse and less structured community. These results suggest that the combination of intensive land use under future climatic conditions may shape soil food webs in a way that compromises plant growth and other important ecosystem functions.

In general, total nematode densities increased under future climatic conditions. While climate was often shown to have only weak effects on nematode densities (Cesarz et al. 2015; De Long et al. 2016; Siebert et al. 2019a), the positive effects we found in our study contradict a large body of literature reporting negative effects under warmed and/or drought conditions (Dong et al. 2013; Kardol et al. 2010; Yan et al. 2017). Intensive land-use management also led to higher nematode densities, which was surprising as well, given the known susceptibility of soil nematodes to land-use intensification that was confirmed by many previous studies (Dong et al. 2013; Mulder et al. 2003; Okada and Harada 2007; Thomas 1978). A closer look at the feeding groups and functional guilds revealed complex shifts in community composition that were driven by the two interacting global change drivers, likely changing the functioning of communities and highlighting the importance of multifactorial investigations. Based on the multitude of trophic levels and life-history strategies covered by nematodes, we found varying responses with distinct temporal patterns. For instance, nematode indices that reflect the overall state of the ecosystem (Ferris et al. 2001) revealed complex seasonal dynamics with generally enriched and bacteria dominated food webs in fall. Such enrichment is usually caused by high mortality rates after unfavorable conditions (i.e., disturbances) that opportunistic species can benefit from (Ferris et al. 1996, 2001). This is particularly true for species in the fast

bacterial decomposition channel that efficiently use easily degradable substrates and rapidly increase in numbers as soon as food availability allows, whereas the slower fungal decomposition remains dependent on more complex material with high cellulose and lignin content (Bongers 1990; Bongers and Bongers 1998; Bongers and Ferris 1999; Ferris et al. 2001). Indeed, our results for the highly opportunistic Ba₁-nematodes confirm higher numbers in fall compared to the spring samplings (Fig. S4a). In addition, data on microbial activity shows significantly higher activity levels in fall compared to spring (Table S5, Fig. S5), which likely provided the basis for the rise in opportunistic bacterial-feeding nematodes. This pattern may be a consequence of the combined effects of the climate treatment over summer (June–August) when soil organisms were exposed to 20% less precipitation and ~0.6 °C soil and air warming (Fig. S2). Based on soil moisture data for spring, summer, and fall (Table S6, Fig. S6), the severe environmental conditions in summer may still be reflected by a highly disturbed nematode community in our sampling campaign in fall, even though the precipitation treatment was then already changed to an increase in rainfall. Similar results are reported in a study by Kardol et al. (2010), in which it was assumed that 10% soil water content marks a critical threshold for nematode survival and reproduction, rapidly becoming detrimental when approaching 5% (Fig. S6). Thus, a combination of air and soil warming and reduced precipitation may affect the community structure of nematodes in a way that cannot be compensated during more favorable conditions in fall (Bakonyi et al. 2007; Colagiero 2011; Dong et al. 2013; Yan et al. 2017).

Another significant community alteration could be observed in response to intensive grassland management. Whereas bacteria feeders and fungal feeders showed low densities on this land-use type, plant feeders particularly thrived in intensive meadows, reaching by far their highest abundances (especially plant feeders within the cp2 and cp3 classes, Fig. S3, Table S3). As many plant-feeding nematodes are classified as agricultural pests, which can impair plant growth above- and belowground, subsequently putting stable crop yields at risk (Evans et al. 1993; Mueller et al. 2016; Nicol et al. 2011), it is critical to understand their population dynamics under different land-use scenarios. Ratio analyses indicated that the high numbers of plant-feeding nematodes in intensively used grasslands may in fact present a threat to plant productivity (Eisenhauer et al. 2011; Wasilewska 1997)—a finding that could be alarming for farmers and practitioners. Even without considering the impact of concurrent global change factors, it is estimated that about 10% of the world's crop production is reduced by the activities of plant-feeding nematodes (Smiley and Nicol 2009; Whitehead 1997). To prevent yield losses by nematode species feeding on plant tissues and harming their roots

(Neher 2010), the control by natural antagonists, including predatory nematodes, can be among the most effective and sustainable measures (Neher 2010) as a well-structured soil food web may be able to regulate the rise of opportunistic species and pest nematodes (Doran and Parkin 1994; Ferris et al. 2001; Kennedy and Smith 1995). However, we are aware of the fact that differences in plant biomass among the land-use types (see for example Siebert et al. (2019b)) may also be accountable for varying abundances of plant-feeding nematodes and may induce bottom-up effects on the nematode community. However, as we currently lack an assessment of herbivory pressure that would allow us to draw strong conclusions about top-down effects of plant-feeding nematodes on plant growth, we need to be cautious when discussing potential effects of rises in plant-feeding nematodes. Future research can address this knowledge gap by performing plant–soil feedback experiments, manipulating the nematode community structure in controlled mesocosm studies, or by determining herbivory pressure through energy flux calculations (Barnes et al. 2018).

Notably, we detected large differences in the structure of nematode communities between land-use types, mainly separating poorly structured communities in farmlands from those in grasslands. In grasslands, we also found more mature nematode communities with higher abundances of predators and omnivorous species. This is in line with the general expectation that land-use types associated with frequent fertilization, ploughing, and highly productive monocultures are leading to simplified communities with a dominance of opportunistic taxa that can withstand such conditions (Bongers and Bongers 1998; Dmowska and Kozłowska 1988). There is strong evidence that complex, highly structured, and mature nematode assemblages are more capable to ensure the stable provisioning of diverse ecosystem functions under environmental stress and to recover after disturbances, e.g., due to functional redundancy and/or higher connectance (Ferris et al. 2001; Menge 1995; Strong 1992; Wardle et al. 1995; Yeates and Wardle 1996). To facilitate the continued existence of such highly structured soil food webs and diverse soil nematode communities under environmental disturbances, the role of plant diversity is often highlighted as one avenue to stabilize communities (Hautier et al. 2014; Neher 2010; Wagner et al. 2015), which might then again be able to prevent the rise of plant-feeding, potential pest species (Ferris et al. 2001). However, the nematode communities in the two extensively managed grasslands were not the most mature and structured, but were excelled by the intensive grasslands. Moreover, we could not find clear evidence for buffering effects of land-use types comprising higher plant diversity under future climatic conditions, thus failing to confirm our second hypothesis. In contrast to other studies, which also reported a decrease in the structure of nematode assemblages based

on climate treatments (Porazinska et al. 1999; Thakur et al. 2014), these effects were only marginal in our study.

In accordance with many previous studies (Bongers and Bongers 1998; Briones et al. 1997; Dong et al. 2013; Porazinska et al. 1999; Sánchez-Moreno et al. 2006; Yeates and Bird 1994; Zhang et al. 2012), our findings showed that global change represents a threat to soil biodiversity. Relating to a recent study by Li et al. (2019), in which the authors only found climate effects in natural habitats, we can provide additional evidence that nematode communities are also affected in agricultural systems. Nematode diversity metrics (both taxon richness and Shannon diversity) indicate that while extensive management fosters diverse communities, diversity declines under intensive management. In our study, the extensive grasslands displayed the highest diversity levels, whereas organic farmlands showed the greatest evenness. These findings highlight the value of less disturbed systems that preserve microhabitats in the soil and, therefore, allow more sensitive, often *K*-strategic taxa within the omnivorous and predatory groups to survive (Bongers and Bongers 1998; Dong et al. 2013). Indeed, our results of the respective feeding groups show that higher trophic levels such as predators and omnivores were almost absent in farmlands, but benefitted from extensive land-use management. This underlines the great susceptibility of higher trophic levels, whose long generation times and low fecundity are often incompatible with intensive management practices (Bongers and Bongers 1998; Ferris et al. 2001; Thakur et al. 2014). As a consequence of this strong reduction in omnivores and predators, top-down regulation of lower trophic levels (e.g., opportunists and plant feeders) may be impaired (de Ruiter et al. 1995; Ferris et al. 2001), with heretofore unknown consequences for crop yields (Evans et al. 1993; Mueller et al. 2016; Nicol et al. 2011).

In conclusion, we found the nematode community to be often affected by complex interactions between both global change drivers and seasonal dynamics, while being particularly sensitive to land-use practices. High enrichment levels in fall are indicative of persisting effects of the climatic conditions over summer that may have long-lasting impacts on nematode communities. The high nematode densities we found under the combination of future climatic conditions and conventional farming coincided with a less diverse, structurally simplified community. Future studies should explore the ecological consequences of these shifts in nematode community composition, because they could cause changes in multiple ecosystem functions and reduce the ability of nematode communities to withstand environmental stress.

Acknowledgements We thank the staff of the Bad Lauchstädt Experimental Research Station (especially Ines Merbach and Konrad Kirsch) for their work in maintaining the plots and infrastructures of the Global

Change Experimental Facility (GCEF), and Harald Auge, François Buscot, and Stefan Klotz for their role in setting up the GCEF. We also thank Alla Kavtea, Claudia Breitzkreuz, Tom Künne, Ulrich Pruschitzki, and Thomas Reitz for their support with lab and field work. Financial support came from the German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

Author contribution statement MS is part of the GCEF steering committee that developed the experimental platform. NE conceived the study. JS collected the data. MC identified the nematodes and calculated nematode indices. JS analyzed the data and wrote the manuscript with contributions from MC, MS, and NE.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

References

- Altermann M, Rinklebe J, Merbach I, Körschens M, Langer U, Hofmann B (2005) Chernozem—soil of the year 2005. *J Plant Nutr Soil Sci* 168:725–740
- Bakonyi G et al (2007) Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. *Appl Soil Ecol* 37:31–40
- Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. *Nature* 515:505–511
- Barnes AD et al (2018) Energy flux: the link between multitrophic biodiversity and ecosystem functioning. *Trends Ecol Evol* 33:186–197
- Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823
- Bengtsson J, Ahnström J, Weibull AC (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J Appl Ecol* 42:261–269
- Bernard EC (1992) Soil nematode biodiversity. *Biol Fertil Soils* 14:99–103
- Birkhofer K et al (2011) Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biol Biochem* 43:2200–2207
- Bongers T (1988) The nematodes of the Netherlands. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, 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. *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
- Briones MJJ, Ineson P, Pearce TG (1997) Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. *Appl Soil Ecol* 6:117–134
- Brussaard L, de Ruiter PC, Brown GG (2007) Soil biodiversity for agricultural sustainability. *Agr Ecosyst Environ* 121:233–244. <https://doi.org/10.1016/j.agee.2006.12.013>
- Cesarz S, Reich PB, 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
- Colagiero M (2011) Climate changes and nematodes: expected effects and perspectives for plant protection. *Redia* 94:113–118
- Crowder DW, Northfield TD, Strand MR, Snyder WE (2010) Organic agriculture promotes evenness and natural pest control. *Nature* 466:109
- Culman SW et al (2010) Biodiversity is associated with indicators of soil ecosystem functions over a landscape gradient of agricultural intensification. *Landscape Ecol* 25:1333–1348
- De Long JR, Dorrepaal E, Kardol P, Nilsson M-C, Teuber LM, Wardle DA (2016) Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient. *Ecosystems* 19:339–355
- de Ruiter PC, Neutel A-M, Moore JC (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269:1257–1260
- De Vries FT et al (2012) Land use alters the resistance and resilience of soil food webs to drought. *Nature Climate Change* 2:276–280
- Dendooven L, Patino-Zúniga L, Verhulst N, Luna-Guido M, Marsch R, Govaerts B (2012) Global warming potential of agricultural systems with contrasting tillage and residue management in the central highlands of Mexico. *Agr Ecosyst Environ* 152:50–58
- Díaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Dmowska E, Kozłowska J (1988) Communities of nematodes in soil treated with semi-liquid manure. *Pedobiologia* 32:323–330
- Dong Z, Hou R, Chen Q, Ouyang Z, Ge F (2013) Response of soil nematodes to elevated temperature in conventional and no-tillage cropland systems. *Plant Soil* 373:907–918
- Doran JW, Parkin TB (1994) Defining and assessing soil quality. In: Doran JW, Coleman DC, Bezdicek BF, Stewart BA (eds) *Defining soil quality for a sustainable environment*. SSSA Special Publication 35, Soil Science Society of America, Madison, WI, pp 3–21
- Doscher R et al (2002) The development of the regional coupled ocean-atmosphere model RCAO. *Boreal Environ Res* 7:183–192
- Eisenhauer N, Migunova VD, Ackermann M, Ruess L, Scheu S (2011) Changes in plant species richness induce functional shifts in soil nematode communities in experimental grassland. *PLoS One* 6:e24087
- Evans K, Trudgill DL, Webster JM, Opperman C (1993) *Plant parasitic nematodes in temperate agriculture*. CAB international Wallingford, UK
- Ferris H (2010) Contribution of nematodes to the structure and function of the soil food web. *J Nematol* 42:63
- Ferris H, Eyre M, Venette R, Lau S (1996) Population energetics of bacterial-feeding nematodes: stage-specific development and fecundity rates. *Soil Biol Biochem* 28:271–280
- Ferris H, Bongers T, De Goede R (2001) A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Appl Soil Ecol* 18:13–29
- Foley JA et al (2005) Global consequences of land use. *Science* 309:570–574
- Giller K, Beare M, Lavelle P, Izac A-M, Swift M (1997) Agricultural intensification, soil biodiversity and agroecosystem function. *Appl Soil Ecol* 6:3–16
- Goldenberg SU, Nagelkerken I, Marangon E, Bonnet A, Ferreira CM, Connell SD (2018) Ecological complexity buffers the impacts of future climate on marine consumers. *Nature Climate Change* 8:229–233
- Hautier Y et al (2014) Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508:521
- Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* 348:336–340
- IPCC TSPB, 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
- Isbell F et al (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526:574–577
- Isbell F et al (2017) Benefits of increasing plant diversity in sustainable agroecosystems. *J Ecol* 105:871–879. <https://doi.org/10.1111/1365-2745.12789>
- Jacob D, Podzun R (1997) Sensitivity studies with the regional climate model REMO. *Meteorol Atmos Phys* 63:119–129
- Kardol P, Cregger MA, Company CE, Classen AT (2010) Soil ecosystem functioning under climate change: plant species and community effects. *Ecology* 91:767–781
- Kennedy AC, Smith K (1995) Soil microbial diversity and the sustainability of agricultural soils. *Plant Soil* 170:75–86
- Kerr RA (2007) Global Warming Is Changing the World. *Science* 316:188–190. <https://doi.org/10.1126/science.316.5822.188>
- Li X et al (2019) Agriculture erases climate constraints on soil nematode communities across large spatial scales. *Global Change Biol.* <https://doi.org/10.1111/gcb.14821>
- Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL (2008) Prioritizing climate change adaptation needs for food security in 2030. *Science* 319:607–610. <https://doi.org/10.1126/science.1152339>
- Marinari S, Masciandaro G, Ceccanti B, Grego S (2000) Influence of organic and mineral fertilisers on soil biological and physical properties. *Biores Technol* 72:9–17
- Maxwell SL, Fuller RA, Brooks TM, Watson JE (2016) Biodiversity: the ravages of guns, nets and bulldozers. *Nature* 536:143–145
- Mazancourt C et al (2013) Predicting ecosystem stability from community composition and biodiversity. *Ecol Lett* 16:617–625
- Meinke I et al (2010) Regionaler Klimaatlas Deutschland der Helmholtz-Gemeinschaft informiert im Internet über möglichen künftigen Klimawandel. *Mitteilungen DMG* 2:5–7
- Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol Monogr* 65:21–74
- Mueller KE et al (2016) Elevated CO₂ and warming shift the functional composition of soil nematode communities in a semi-arid grassland. *Soil Biol Biochem* 103:46–51
- Mulder C, Zwart DD, Van Wijnen H, Schouten A, Breure A (2003) Observational and simulated evidence of ecological shifts within the soil nematode community of agroecosystems under conventional and organic farming. *Funct Ecol* 17:516–525
- Murrell EG, Barton BT (2017) Warming alters prey density and biological control in conventional and organic agricultural systems. *Integr Comp Biol* 57:1–13
- Neher DA (2010) Ecology of plant and free-living nematodes in natural and agricultural soil. *Annu Rev Phytopathol* 48:371–394. <https://doi.org/10.1146/annurev-phyto-073009-114439>
- Newbold T et al (2015) Global effects of land use on local terrestrial biodiversity. *Nature* 520:45–50
- Nicol JM, Turner SJ, Coyne D, Den Nijs L, Hockland S, Maafi ZT (2011) Current nematode threats to world agriculture. *Genomics and molecular genetics of plant-nematode interactions*. Springer, Dordrecht, pp 21–43
- Okada H, Harada H (2007) Effects of tillage and fertilizer on nematode communities in a Japanese soybean field. *Appl Soil Ecol* 35:582–598
- Okada H, Harada H, Kadota I (2005) Fungal-feeding habits of six nematode isolates in the genus *Filenchus*. *Soil Biol Biochem* 37:1113–1120
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara R et al. (2013) Package ‘vegan’. *Community Ecology Package, Version 2*. <http://CRAN.R-project.org/package=vegan>
- Porazinska D, Duncan L, McSorley R, Graham J (1999) Nematode communities as indicators of status and processes of a soil ecosystem influenced by agricultural management practices. *Appl Soil Ecol* 13:69–86
- Porazinska DL et al (2003) Relationships at the aboveground–belowground interface: plants, soil biota, and soil processes. *Ecol Monogr* 73:377–395
- Postma-Blauw MB, de Goede RGM, Bloem J, Faber JH, Brussaard L (2010) Soil biota community structure and abundance under agricultural intensification and extensification. *Ecology* 91:460–473
- R Core Team RCT (2017) R: A language and environment for statistical computing. Vienna, Austria; 2014
- Ramirez KS, Craine JM, Fierer N (2010) Nitrogen fertilization inhibits soil microbial respiration regardless of the form of nitrogen applied. *Soil Biol Biochem* 42:2336–2338
- Rockel B, Will A, Hense A (2008) The regional climate model COSMO-CLM (CCLM). *Meteorol Z* 17:347–348
- Ruess L (1995) Studies on the nematode fauna of an acid forest soil: spatial distribution and extraction. *Nematologica* 1:229–239
- Sala OE et al (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Sánchez-Moreno S, Minoshima H, Ferris H, Jackson LE (2006) Linking soil properties and nematode community composition: effects of soil management on soil food webs. *Nematology* 8:703–715
- Schädler M et al (2019) Investigating the consequences of climate change under different land-use regimes—a novel experimental infrastructure. *Ecosphere*. <https://doi.org/10.1002/ecs2.2635>
- Scialabba NE-H, Müller-Lindenlauf M (2010) Organic agriculture and climate change. *Renewable Agric Food Syst* 25:158–169
- Siebert J, Sünemann M, Auge H et al (2019a) The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. *Sci Rep* 9:639. <https://doi.org/10.1038/s41598-018-36777-3>
- Siebert J et al (2019b) Extensive grassland-use sustains high levels of soil biological activity, but does not alleviate detrimental climate change effects. *Adv Ecol Res* 60:25
- Smiley RW, Nicol JM (2009) Nematodes which challenge global wheat production. *Wheat Sci Trade* 10:171–187
- Smith P et al (2016) Global change pressures on soils from land use and management. *Glob Change Biol* 22:1008–1028
- Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754
- Thakur MP et al (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
- Thomas S (1978) Population densities of nematodes under seven tillage regimes. *J Nematol* 10:24
- Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. *Nature* 418:671–677
- Treseder KK (2008) Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecol Lett* 11:1111–1120
- Tsiafouli MA, Thébault E, Sgardelis SP, de Ruiter PC, van der Putten WH, Birkhofer K, Hemerik L, de Vries FT, Bardgett RD, Brady MV, Bjornlund L, Jørgensen HB, Christensen S, Hertefeldt TD, Hotes S, Gera Hol WH, Frouz J, Liiri M, Mortimer SR, Setälä H, Tzanopoulos J, Uteseny K, Pižl V, Stary J, Wolters V, Hedlund K (2015) Intensive agriculture reduces soil biodiversity across Europe. *Glob Change Biol* 21(2):973–985
- Voigt W, Perner J, Hefin Jones T (2007) Using functional groups to investigate community response to environmental changes: two grassland case studies. *Glob Change Biol* 13:1710–1721
- Wagner D, Eisenhauer N, Cesarz S (2015) Plant species richness does not attenuate responses of soil microbial and nematode communities to a flood event. *Soil Biol Biochem* 89:135–149

- Wall DH, Nielsen UN, Six J (2015) Soil biodiversity and human health. *Nature* 528(7580):69–76
- Wardle D, Yeates G, Watson R, Nicholson K (1995) The detritus food-web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. *Plant Soil* 170:35–43
- Wasilewska L (1997) Soil invertebrates as bioindicators, with special reference to soil-inhabiting nematodes. *Russian J Nematol* 5:113–126
- Wheeler T, Von Braun J (2013) Climate change impacts on global food security. *Science* 341:508–513
- Whitehead AG (1997) *Plant nematode control*. CAB International, Wallingford (UK)
- Wilby A, Thomas MB (2002) Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecol Lett* 5:353–360
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci* 96:1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Yagioka A, Komatsuzaki M, Kaneko N, Ueno H (2015) Effect of no-tillage with weed cover mulching versus conventional tillage on global warming potential and nitrate leaching. *Agr Ecosyst Environ* 200:42–53
- Yan X, Wang K, Song L, Wang X, Wu D (2017) Daytime warming has stronger negative effects on soil nematodes than night-time warming. *Sci Rep* 7:44888
- Yeates G, Bird A (1994) Some observations on the influence of agricultural practices on the nematode faunas of some South Australian soils. *Fundam Appl Nematol* 17:133–145
- Yeates G, Wardle D (1996) Nematodes as predators and prey: relationships to biological control and soil processes. *Pedobiologia* 40:43–50
- 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. *J Nematol* 25:315
- Yeates G, Wardle D, Watson R (1999) Responses of soil nematode populations, community structure, diversity and temporal variability to agricultural intensification over a seven-year period. *Soil Biol Biochem* 31:1721–1733
- Yeates G, Dando J, Shepherd T (2002) Pressure plate studies to determine how moisture affects access of bacterial-feeding nematodes to food in soil. *Eur J Soil Sci* 53:355–365
- Zhang X, Li Q, Zhu A, Liang W, Zhang J, Steinberger Y (2012) Effects of tillage and residue management on soil nematode communities in North China. *Ecol Ind* 13:75–81