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Global patterns and controls of soil nematode responses to nitrogen enrichment: A meta-analysis

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ABSTRACT

Nematodes are important components of soil food webs and have important ecosystem functions. However, the responses of soil nematode communities to nitrogen (N) deposition have not been well assessed over large spatial scales. Here, we conducted a global-scale meta-analysis of the effects of N-addition regimes (N form, N addition approach, and N addition rate) and environmental factors (ecosystem type, soil depth, climate, and soil property) on the responses of soil nematodes to N addition. The results showed that N addition significantly increased the relative abundance of bacterial-feeding nematodes (23.54%), but decreased the relative abundance of plant-feeding nematodes (−20.24%) and omnivorous-predatory nematodes (−22.28%). Nitrogen addition, however, did not significantly affect total nematode abundance or the relative abundance of fungal-feeding nematodes. Understory N addition usually had larger effects on nematode abundance than canopy N addition. The responses to N addition increased with N addition rate in the case of bacterial-feeding nematode abundance, but decreased with N addition rate in the case of plant-feeding nematode and fungal-feeding nematode abundances. Nematode abundance in grasslands were more responsive to N addition than in forests or croplands, and the responses were affected by soil depth. The response ratios of bacterial-feeding nematodes to N addition decreased with increases in mean annual temperature and mean annual precipitation, while the response ratios of plant-feeding nematodes showed the opposite trend. Soil pH and organic carbon did not affect the response ratios of nematode parameters to N addition except plant parasite index. In summary, the responses of soil nematodes to N addition on a global scale were found to be affected by both N-addition regimes and environmental factors. We suggest that our understanding of how N deposition affects soil nematodes will be increased by additional studies of canopy N addition and of tropical ecosystems.

1. Introduction

Atmospheric reactive nitrogen (N) deposition, a global problem resulting mainly from fossil fuel combustion and agricultural fertilizer application, has substantially increased over the past century and is evaluated to be as high as 93.6 Tg N yr^{-1} in 2016 (Galloway et al., 2008; Ackerman et al., 2019). Extensive N inputs have dramatically changed terrestrial ecosystem processes including soil biota community dynamics and nutrient cycling (Treseder, 2008; Leff et al., 2015; Yu et al., 2019). It is therefore important to increase our understanding of how N enrichment affects soil ecosystem components and functions.

Nematodes are key components of terrestrial ecosystem and occupy all trophic levels of soil food webs (van den Hoogen et al., 2019). Based on feeding characteristics, nematode families can be classified into five trophic groups, i.e., bacterial-feeding nematodes, fungal-feeding nematodes, plant-feeding nematodes, and omnivorous-predatory nematodes

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(Bongers and Bongers, 1998). Soil nematodes can regulate ecosystem processes by feeding on microorganisms (Crowther et al., 2011; Zhou et al., 2020), and their abundances and activities are closely correlated with biogeochemical cycles such as nutrient mineralization and carbon dynamics (Ferris, 2010; Neher et al., 2012; Wang et al., 2021). Because nematodes can move only in environments with continuous soil water films, their activities are greatly affected by soil texture, moisture, and other soil properties (Yeates and Bongers, 1999). In addition, nematodes are vulnerable to external disturbances and environmental changes, such as land-use change, soil pollution, and farm management (Wei et al., 2012; Treonis et al., 2018). As a result, nematodes are considered to be useful indicators of soil food webs and ecosystem health (Neher, 2001; Zhao et al., 2013).

Previous studies have widely reported the effects of N addition on the abundance, community diversity, and ecological indices of soil nematodes (Lokupitiya et al., 2000; Liang et al., 2009; Zhao et al., 2014; Shaw et al., 2019), and the responses of soil nematode abundance and diversity to N addition are directly affected by N form, N addition rate, and N addition method (Forge et al., 2005; Gruzdeva et al., 2007; Wei et al., 2012; Pan et al., 2015). For example, nitrate but not ammonium, significantly increased nematode diversity and the relative abundance of bacterial-feeding nematodes, but decreased nematode dominance and the relative abundance of plant-feeding nematodes in a cropland (Pan et al., 2015). In addition, the abundances of all nematode trophic groups decreased with increasing N application rate (Wei et al., 2012). Researchers generally investigate the effects of N addition by adding N to the understory. Research in forests has shown, however, that a significant proportion of atmospheric N deposition is retained by the forest canopy, indicating that understory N addition in forests is likely to overestimate the effects of N on soil nematodes and other components of the soil food web (Liu et al., 2020). N-induced changes in soil nutrient status and belowground community structure can change nematode functional composition, nematode taxon richness, and the stability of soil food webs (Chen et al., 2015; Mao et al., 2017; Peng et al., 2017).

The responses of nematodes to N addition are greatly affected by environmental factors, e.g., ecosystem types, soil properties, soil depth, temperature, and precipitation. According to previous studies, the responses of soil nematodes to N addition are usually greater in grasslands than in forests (Zhao et al., 2014; Chen et al., 2015; Ma et al., 2018). Long-term N addition could change soil pH and edaphic conditions (Högberg et al., 2006), as well as suppress the decomposition of soil organic matter and enhance soil carbon accumulation (Tonitto et al., 2014), which would in turn affect nematode abundance and community structure (Chen et al., 2015). Nematode trophic groups respond differently to moisture and temperature variations in different soil layers (Zhang et al., 2020). Because moisture is often closely correlated with temperature in global-change scenarios (Lu et al., 2018), research on the effects of N addition on soil nematodes should therefore consider moisture and temperature. By altering interactions among trophic levels in soil food webs, anthropogenic N deposition can alter the diversity of soil nematode communities (Shao et al., 2017; Shaw et al., 2019). However, the belowground food web is complex, and the changes may result from multiple pathways that remain to be elucidated. Previous studies have focused on regional patterns, or conducted a global synthesis on nematode communities as affected by N addition, chemical fertilizer and organic fertilizer in cropland ecosystem (Liu et al., 2016a), but whether and how independent N addition affects soil nematodes and their functional feature across different ecosystem types, N forms, and N addition methods at a global scale remains unclear.

In the current study, we conducted a meta-analysis of soil nematode responses to N addition in order to determine the effects of N-addition regimes (N form, N addition rate, and N addition method) and environmental factors (ecosystem type, soil depth, climate, and soil property) on responses of soil nematodes to N addition. We attempted to answer the following questions: (a) What are the global trends of N effects on soil nematodes? (b) How do N-addition regimes and environmental factors affect soil nematode responses to N addition? and (c) What is the relative importance of N-addition regimes and environmental factors in determining the responses of soil nematodes to N addition at a global scale?

2. Materials and methods

2.1. Data sources

Data were collected by searching published peer-reviewed articles and Chinese dissertations that reported nematode responses to N addition in the Web of Science (http://apps.webofknowledge.com/) and the China National Knowledge Infrastructure Database (http://www.cnki.net/) up to 11 May 2020. The following keywords/phrases were used: "nitrogen addition" or "nitrogen fertilization" or "nitrogen deposition" or "fertilizer" or "fertilization"; and "soil nematode" or "nematode community" or "nematodes" or "soil fauna". The gathered publications were further screened based on four criteria: (a) only field experiments were considered, and the experiments had to include at least three replicates; (b) when the same experiment was reported in two publications, e.g., scientific article and dissertation from the same author, only one dataset was retained; (c) measurements at different sites or under different climatic conditions or different N treatments were regarded as independent experiments; and (d) when multiple time points were reported for one study, the final time point was selected. A total of 52 studies containing 220 observations were finally selected (Fig. 1 shows the geographical distribution of the study sites).

Data for the abundance of nematode trophic groups, nematode diversity, and nematode ecological indices were directly collected from texts and tables in the original studies or were extracted from figures using GetData (version 2.25). Nematode abundances were total nematode abundance and the relative abundance of nematode trophic groups, including bacterial-feeding nematodes, fungal-feeding nematodes, plant-feeding nematodes, and omnivorous-predatory nematodes. Diversity indices were Shannon-Wiener diversity (H′) and Simpson dominance (λ). Nematode ecological indices were the maturity index (MI), plant parasite index (PPI), structure index (SI), and enrichment index (EI). We also collected treatment information (mainly N-addition regimes, i.e., N form, application method, addition rate, and study duration) and site-specific information including ecosystem type, soil depth, latitude, longitude, mean annual temperature, mean annual precipitation, and soil properties from the original studies. We expressed N-addition rate in terms of "kg ha^{-1} year^{-1}" and N-application duration in terms of "year". The data of mean annual temperature and mean annual precipitation were obtained from the online climatic database (https://www.worldclim.org/) if not provided in the articles.

2.2. Data analysis

We conducted a meta-analysis of the effects of N addition on soil nematodes. The effect sizes of N addition for soil nematode community parameters were estimated using the natural logarithm of the response ratio (lnRR):

$$\mathrm{lnRR} = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) = ln\left(\overline{X}_t\right) - ln\left(\overline{X}_c\right)$$

where $\overline{X}_t$ and $\overline{X}_c$ are the means of the treatments and controls, respectively.

Because standard deviations were not indicated in some of the studies, individual observations were weighted by the number of experimental replicates (Adams et al., 1997; Pittelkow et al., 2015), calculated as:

$$w = \frac{n_t \times n_c}{n_t + n_c}$$

Fig. 1. Locations of the data points collected in this meta-analysis. The sizes of data points stand for the numbers of independent experiments.

where n_t and n_c are the number of replicated observations in the treatment group and control group, respectively.

The 95% confidence interval (CI) for the effect-size estimate was calculated by bootstrapping techniques, and was used to determine the significance of the response. If the 95% Bootstrap CI values did not overlap with zero, the responses of soil nematodes to N addition were considered to be significant ($P < 0.05$) and to represent a significant increase (>0, on the right of zero) or a significant decrease (<0, on the left of zero). Meta-analyses were conducted using MetaWin 2.1. To better explain the responses of soil nematodes to N addition as affected by N form, N approach, ecosystem type, and soil depth, we converted the weighted response ratio ($\ln RR_{++}$) into the percentage of change with the following equation:

$$\text{Change}\ \ (\%) = [\exp(lnRR_{++}) - 1] \times 100\%$$

Linear regression models were used to examine the relationships between response ratios and N addition rate and environmental factors, including mean annual temperature, mean annual precipitation, pH, and soil organic carbon (SOC). The relative importance of assessed factors (i.e., N form, application method, addition rate, study duration, ecosystem type, soil depth, latitude, longitude, pH, SOC, mean annual temperature, and mean annual precipitation) were included in a model selection analysis calculated with the R package 'glmulti'; relative importance was indicated by the sum of Akaike weights for all models that contained the factor in question. The sum can be considered an indication of the overall ability of a single factor to explain the variation in a response ratio across all models. The most important variables were identified at a cutoff of 0.8 (Chen et al., 2018, 2020). R package 'stats' was used for linear regression analysis (Collyer et al., 2018), and model significance was set at $P < 0.05$. Sigmaplot 12.5 was used for graphing.

3. Results

3.1. Nematode responses to N addition as affected by N-addition regimes

Overall and at a global scale, N addition increased the abundance of bacterial-feeding nematodes (by 23.54% [95% CI: 14.63%–33.15%], $N = 191$), decreased the abundances of plant-feeding nematodes (by 20.24% [95% CI: 13.97%–26.07%], $N = 186$) and omnivorous-predatory nematodes (by 22.28% [95% CI: 16.15%–27.98%], $N = 180$), but did not change the abundances of total nematodes or fungal-feeding nematodes (Fig. 2A). In terms of N sources, NH_4NO_3 usually had larger effects than urea [$CO(NH_2)_2$] and other N sources. Addition of NH_4NO_3 had significant positive effects on total nematode abundance (by 10.04% [95% CI: 1.27%–19.58%], $N = 130$) and the abundance of bacterial-feeding nematodes (by 35.53% [95% CI: 22.90%–49.45%], $N = 119$), but had negative effects on the abundances of plant-feeding nematodes (by 26.99% [95% CI: 20.49%–32.96%], $N = 115$) and omnivorous-predatory nematodes (by 24.23% [95% CI: 17.56%–30.37%], $N = 118$). Addition of urea only reduced the abundance of omnivorous-predatory nematodes (by 24.32% [95% CI: 3.59%–40.59%], $N = 35$). As noted earlier, any N form did not affect the abundance of fungal-feeding nematodes, nematode diversity indices, and ecological indices.

Understory N addition did not significantly affect total nematode abundance but significantly affected the abundances of all nematode trophic groups (Fig. 2B). Understory N addition increased the abundance of bacterial-feeding nematodes (by 24.71% [95% CI: 15.50%–34.65%], $N = 175$), but reduced the abundances of fungal-feeding nematodes (by 11.71% [95% CI: 0.85%–21.38%], $N = 175$), plant-feeding nematodes (by 20.98% [95% CI: 14.61%–26.88%], $N = 170$), and omnivorous-predatory nematodes (by 22.24% [95% CI: 15.94%–28.07%], $N = 164$). Canopy N addition did not affect nematode abundance. Any N addition approach did not affect nematode diversity and ecological indices.

There were positive relationships between N addition rate and the response ratios of bacterial-feeding nematodes abundance ($R^2 = 0.081$, $P < 0.001$, and $N = 191$; Fig. 3b), and negative relationships between N addition rate and the response ratios of abundances of fungal-feeding nematodes ($R^2 = 0.034$, $P = 0.011$, and $N = 191$; Fig. 3c) and plant-feeding nematodes ($R^2 = 0.046$, $P = 0.003$, and $N = 186$; Fig. 3d). However, N addition rate did not affect the response ratios of total nematode abundance and the abundance of omnivorous-predatory nematodes ($P > 0.05$; Fig. 3a and e).

3.2. Nematode responses to N addition as affected by environmental factors

Most studies sampled the 0–20 cm soil layer, and only a few studies sampled the 0–5 cm soil layer (Fig. 2C). In the 0–5 cm soil layer, N addition had significant positive effects on the abundances of total

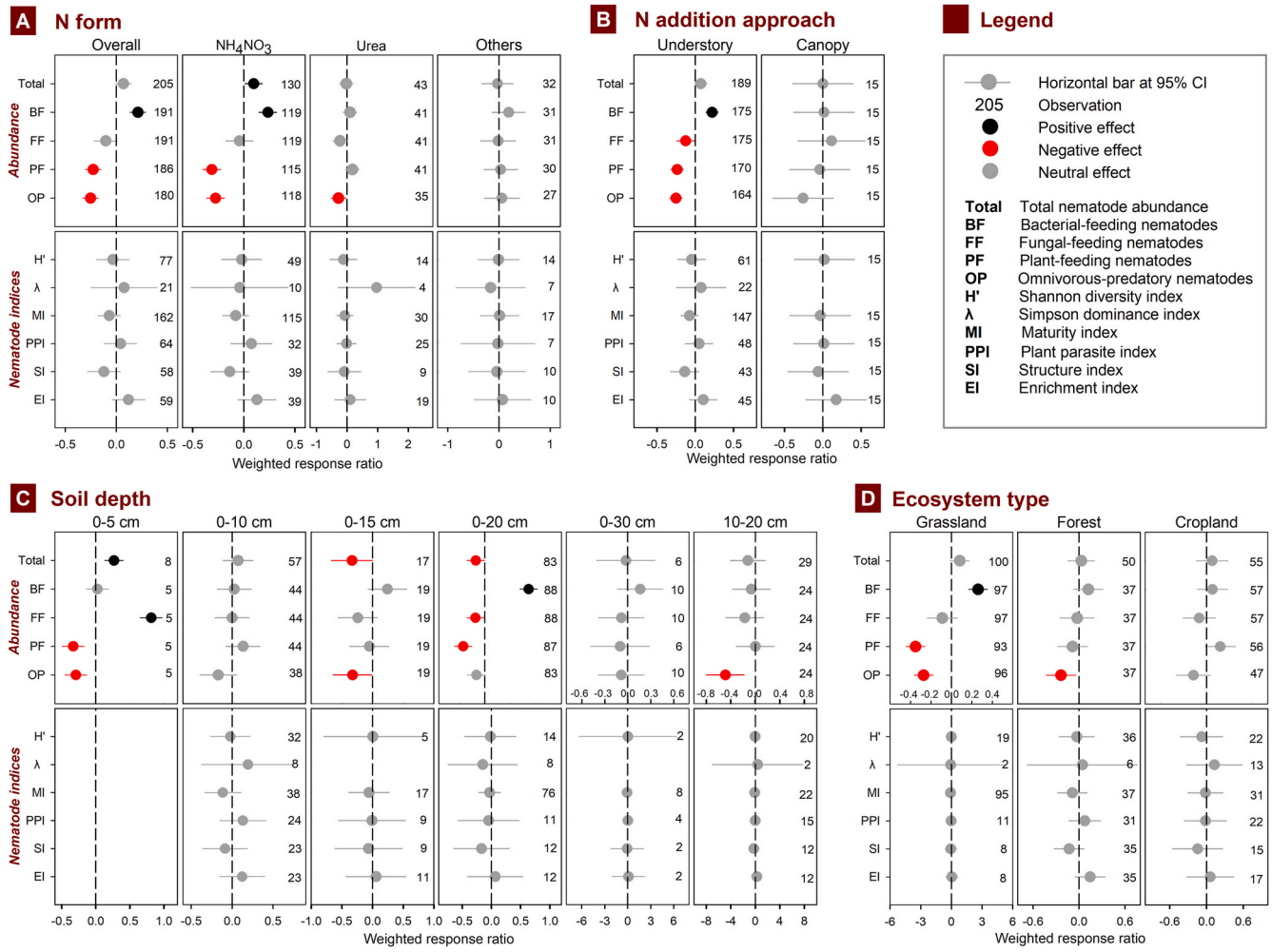

Fig. 2. Effects of different nitrogen forms (A), addition approach (B), soil depths (C), and ecosystem types (D) on soil nematode community parameters. Under nitrogen form, others include slow-release urea, calcium nitrate, calcium cyanamide, calcium ammonium nitrate, and those not indicated in original case studies. Error bars represent 95% confidence intervals (CI) of the weighted percentage change. The black and red circles represent significant positive and negative effects, respectively (95% CI not overlapping with zero), and the grey circles represent non-significant effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

nematodes (by 30.51% [95% CI: 14.21%–49.12%], $N = 8$) and fungal-feeding nematodes (by 125.33% [95% CI: 92.23%–164.11%], $N = 5$). In the 0–20 cm soil layer, N addition significantly increased the abundance of bacterial-feeding nematodes (by 135.61% [95% CI: 99.29%–178.54%], $N = 88$), but decreased the abundances of total nematodes (by 16.20% [95% CI: 0.29%–29.57%], $N = 83$), fungal-feeding nematodes (by 16.72% [95% CI: 1.55%–29.56%], $N = 88$), and plant-feeding nematodes (by 34.49% [95% CI: 22.45%–44.65%], $N = 87$). Nematode abundance did not change in response to N addition in the 0–30 cm soil layer. N addition did not affect nematode diversity and ecological indices in all the soil depths.

For grasslands, N addition increased the abundance of bacterial-feeding nematodes (by 29.91% [95% CI: 18.63%–42.29%], $N = 97$), but decreased the abundance of plant-feeding nematodes (by 29.55% [95% CI: 22.74%–35.76%], $N = 93$) and the abundance of omnivorous-predatory nematodes (by 23.73% [95% CI: 16.46%–30.37%], $N = 96$). For forests, N addition decreased the abundance of omnivorous-predatory nematodes (by 20.94% [95% CI: 4.32%–34.68%], $N = 37$). However, the abundances of all the trophic groups did not change in response to N addition in croplands. N addition did not affect nematode diversity and ecological indices in grasslands, forests, and croplands (Fig. 2D).

The response ratios of total nematode abundance ($R^2 = 0.054$, $P = 0.001$, and $N = 204$; Fig. 4a) and the abundance of plant-feeding nematodes ($R^2 = 0.102$, $P < 0.001$, and $N = 185$; Fig. 4d) to N addition increased as mean annual temperature increased, while the response ratios of the abundance of bacterial-feeding nematodes to N addition decreased as mean annual temperature increased ($R^2 = 0.182$, $P < 0.001$, and $N = 189$; Fig. 4b). Mean annual temperature did not affect the response ratios of the abundances of fungal-feeding and omnivorous-predatory nematodes to N addition ($P > 0.05$; Fig. 4c and e).

The response ratios of the abundance of bacterial-feeding nematodes to N addition decreased ($R^2 = 0.038$, $P = 0.007$, and $N = 191$; Fig. 4g), but the response ratios of the abundance of plant-feeding nematodes to N addition increased ($R^2 = 0.038$, $P = 0.007$, and $N = 186$; Fig. 4i) as mean annual precipitation increased. Mean annual precipitation did not affect the response ratios of total nematode abundance, and the abundances of fungal-feeding and omnivorous-predatory nematodes ($P > 0.05$; Fig. 4f, h and j).

The response ratios of plant parasite index to N addition decreased as pH increased ($R^2 = 0.27$, $P = 0.004$, and $N = 29$; Table 1). Except the plant parasite index, the response ratios of other nematode ecological indices, the diversity indices, and nematode abundance did not response to pH. Soil organic carbon did not affect the response ratios of nematode abundance, nematode diversity indices, and ecological indices.

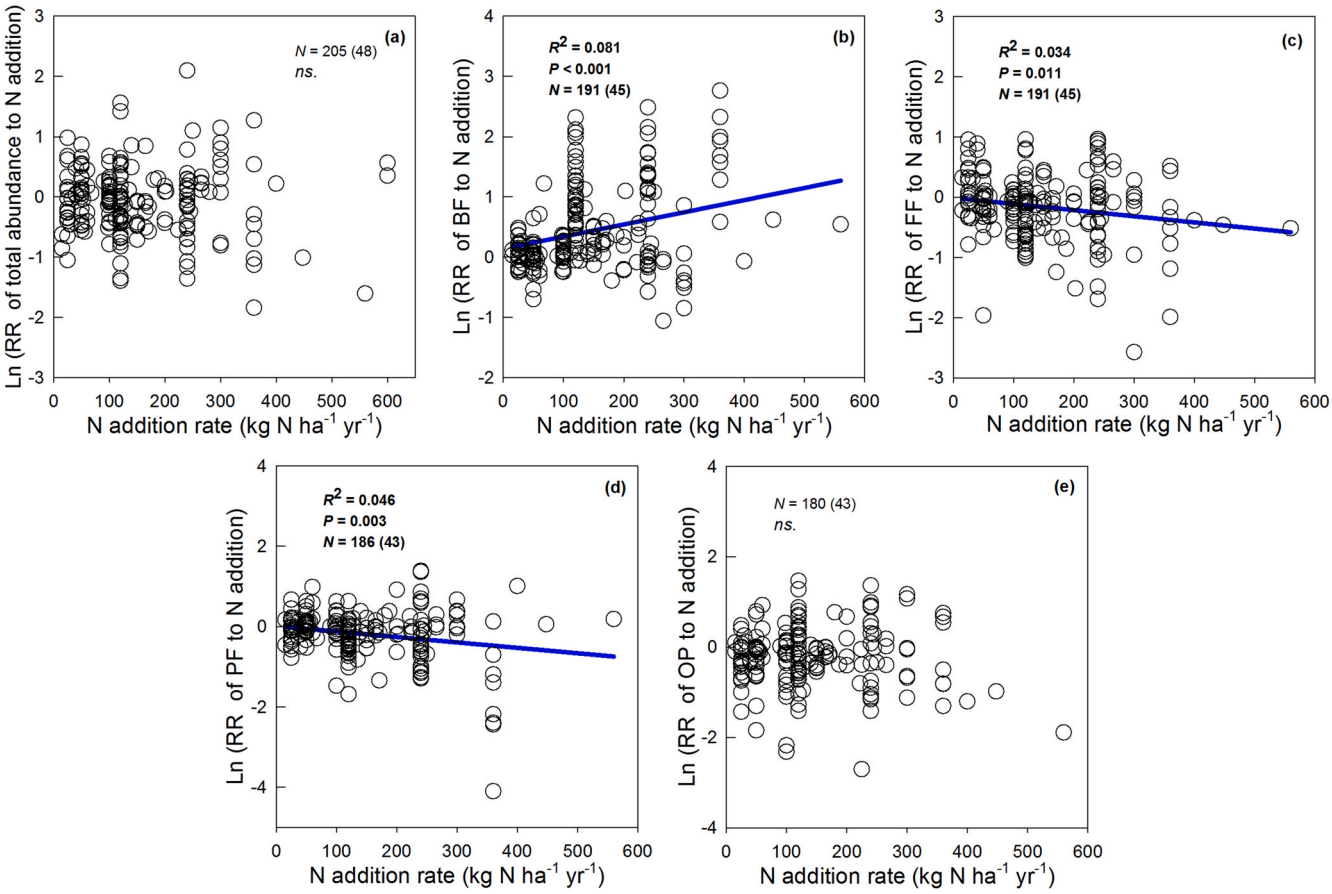

Fig. 3. Regression models of the response ratios of nematode abundance with N addition rate. BF: bacterial-feeding nematodes; FF: fungal-feeding nematodes; PF: plant-feeding nematodes; OP: omnivorous-predatory nematodes; 205 (48): observation (study number).

3.3. Importance of variables in the responses of nematode trophic groups to N addition

The Akaike-weights models showed that both environmental factors and N-addition regimes affected the responses of nematode abundance to N addition (Fig. 5). The effects of N addition were best explained by soil depth and experimental duration for total nematode abundance (Fig. 5a); by N addition rate, soil depth, ecosystem type, and mean annual temperature for the abundance of bacterial-feeding nematodes (Fig. 5b); by soil depth, N addition rate, and mean annual precipitation for the abundance of fungal-feeding nematodes (Fig. 5c); and by ecosystem type and mean annual temperature for the abundances of plant-feeding and omnivorous-predatory nematodes, respectively (Fig. 5d, and e).

4. Discussion

4.1. Nematode responses to N-addition regimes

In the present meta-analysis of the effects of N addition on soil nematodes, we considered three properties of N-addition regimes: N form, N application method, and N addition rate. We found that NH_4NO_3 and urea were the most widely used N sources, and NH_4NO_3 had larger effects on soil nematodes than urea. Nitrate fertilizer inputs to soil can generally be absorbed by plant roots, and assimilated and denitrified by soil microorganisms (Pan et al., 2008). An increase in available N can increase microbial activity and numbers, which can in turn promote bacterial-feeding nematodes (which tend to be *r*-strategists and to be better colonizers than persisters, i.e., to have low "colonizer-persistence" values, commonly termed c-p values), but inhibit plant-feeding nematodes and omnivorous-predatory nematodes (which tend to be *K*-strategists with high c-p values, i.e., poor colonizers but good persisters) (Bongers et al., 1997; Liang et al., 2009). Accordingly, our meta-analysis revealed a significant positive effect of N addition on the abundance of bacterial-feeding nematodes (most of which have low c-p values), but a significant negative effect on the abundance of omnivorous-predatory nematodes (most of which have high c-p values). Besides, our meta-analysis indicated that the application of NH_4NO_3 reduced the abundance of plant-feeding nematodes. One explanation is that the addition of ammoniacal N and nitrate N can improve plant health and defenses and thereby increase plant resistance (Zhang et al., 2009; Pan et al., 2015), which as a result increases the difficulty of plant-feeding nematodes to obtain food. Another possible reason is that high levels of N to soil could suppress plant richness and thereby provide less food for plant-feeding nematodes and consequently decrease their abundance (Aber et al., 1998; Wu et al., 2013). Accordingly, the response ratios of the abundance of plant-feeding nematodes to N addition significantly decreased as the N addition rate increased. Similarly, the response ratios of the abundance of fungal-feeding nematodes to N addition significantly decreased with increasing N addition rate, which is reasonable because fungal biomass was reported to decline in response to N addition (Treseder, 2008).

Both abiotic factors and food resources can strongly effect omnivorous-predatory nematodes, and abiotic factors usually play more critical roles than food resources (Chen et al., 2013; Liu et al., 2016b). Therefore, N addition decreased the abundance of omnivorous-predatory nematodes in our study. Furthermore, the long-lived trophic groups with higher c-p values, e.g., omnivorous-predatory nematodes, are generally sensitive to environmental disturbance (Ferris et al., 2001; Liu et al., 2016b). For instance,

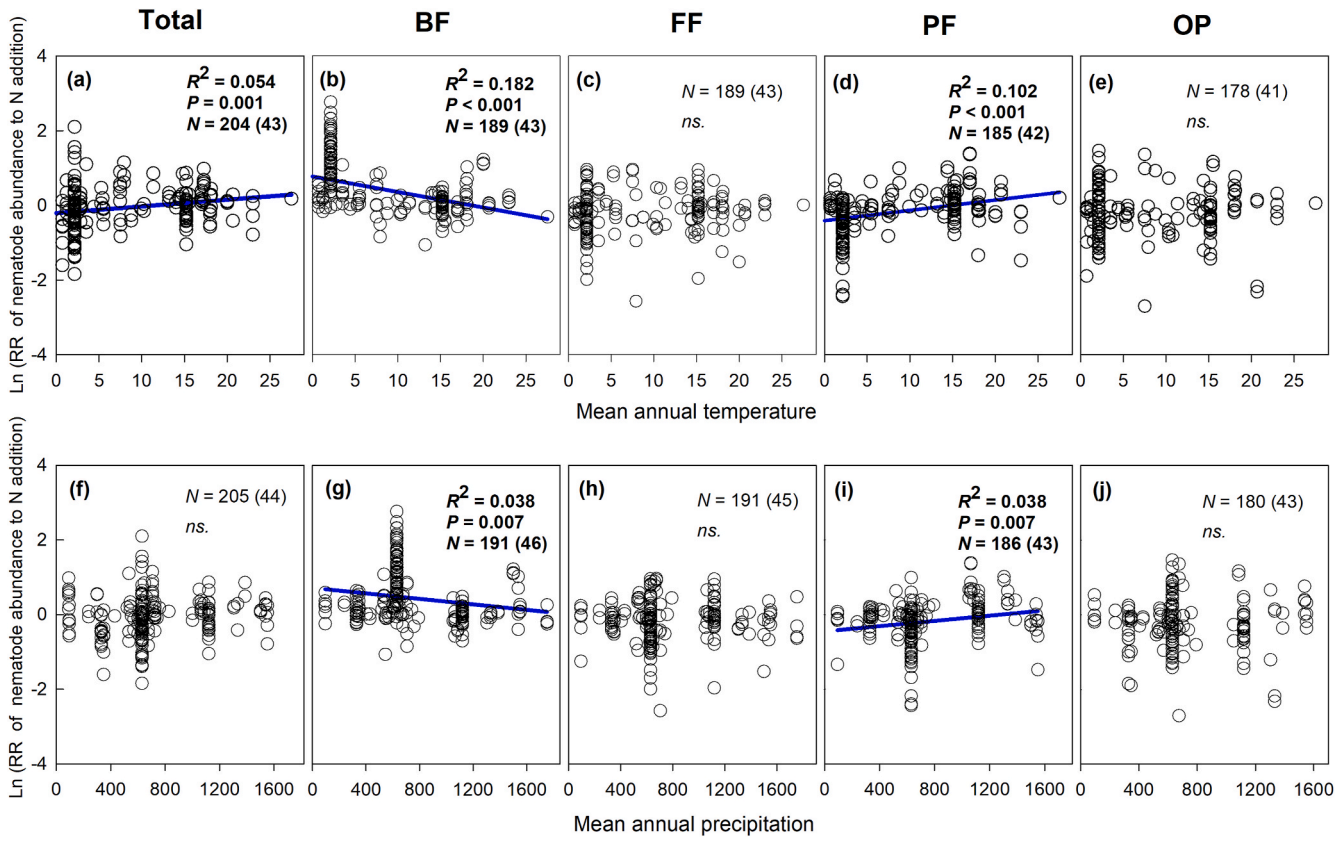

Fig. 4. Regression models of the response ratio of nematode abundance to mean annual temperature and mean annual precipitation. Total: total nematode abundance; BF: bacterial-feeding nematodes; FF: fungal-feeding nematodes; PF: plant-feeding nematodes; OP: omnivorous-predatory nematodes; 204 (43): observation (study number).

Table 1
Results of regression models of the response ratio of soil nematode community parameters to N addition against pH and soil organic carbon (SOC).

Independent variable (x)	Dependent variable (y)	Observation	Study number	R^2	*P*	Independent variable (x)	Dependent variable (y)	Observation	Study number	R^2	*P*
pH	Total	77	26	0.02	0.22	SOC	Total	53	17	0.03	0.84
	BF	61	25	0.01	0.54		BF	37	15	0.01	0.62
	FF	61	25	0.001	0.85		FF	37	15	0.03	0.29
	PF	61	25	0.05	0.08		PF	37	15	0.003	0.76
	OP	57	24	0.02	0.34		OP	33	14	0.005	0.70
	H′	34	12	0.002	0.80		H′	16	7	0.19	0.09
	λ	12	6	0.31	0.06		λ	10	4	0.001	0.93
	MI	49	19	0.02	0.37		MI	29	12	0.003	0.78
	PPI	29	12	**0.27**	**0.004**		PPI	16	8	0.05	0.39
	SI	28	11	0.03	0.36		SI	15	6	0.03	0.56
	EI	30	12	0.10	0.09		EI	15	6	0.16	0.15

Notes: Total: total nematode abundance; BF: bacterial-feeding nematodes; FF: fungal-feeding nematodes; PF: plant-feeding nematodes; OP: omnivorous-predatory nematodes; H': Shannon diversity index; λ: Simpson dominance index; MI: maturity index; PPI: plant parasite index: SI: structure index; EI: enrichment index. Declaration of interests.

both N sources of NH_4NO_3 and urea reduced the abundance of omnivorous-predatory nematodes (Hu and Qi, 2010; Wei et al., 2012; Pan et al., 2015), which is consistent with our perspective. Although N application had a slightly positive effect on total nematode abundance, some opposite responses to N addition among omnivorous-predatory nematodes, bacterial-feeding nematodes, and plant-feeding nematodes were detected; this balancing or trade-off would contribute to the weak response of total nematode abundance to N addition.

Unlike understory N addition, canopy N addition did not apparently affect nematode abundance, diversity and ecological indices in forests. The lack of effects of canopy N addition may be due to the interception of N by the forest canopy (Liu et al., 2020). On the other hand, fewer studies involved canopy N addition ($N = 15$) than understory N addition (at least 164). The small sample size can at partially explain the smaller response ratios to canopy addition of N than to understory addition of N. Additional experiments are needed to clarify the effects of canopy addition of N on soil nematodes.

4.2. Responses of nematodes to N addition as affected by environmental factors

It is notable that N addition had greater effects on more nematode trophic groups in grasslands than in forests or croplands. One possible explanation involves the global distribution and functional composition of soil nematodes. Soil nematodes are more abundant in boreal and temperate forests than in grasslands, presumably because of the greater

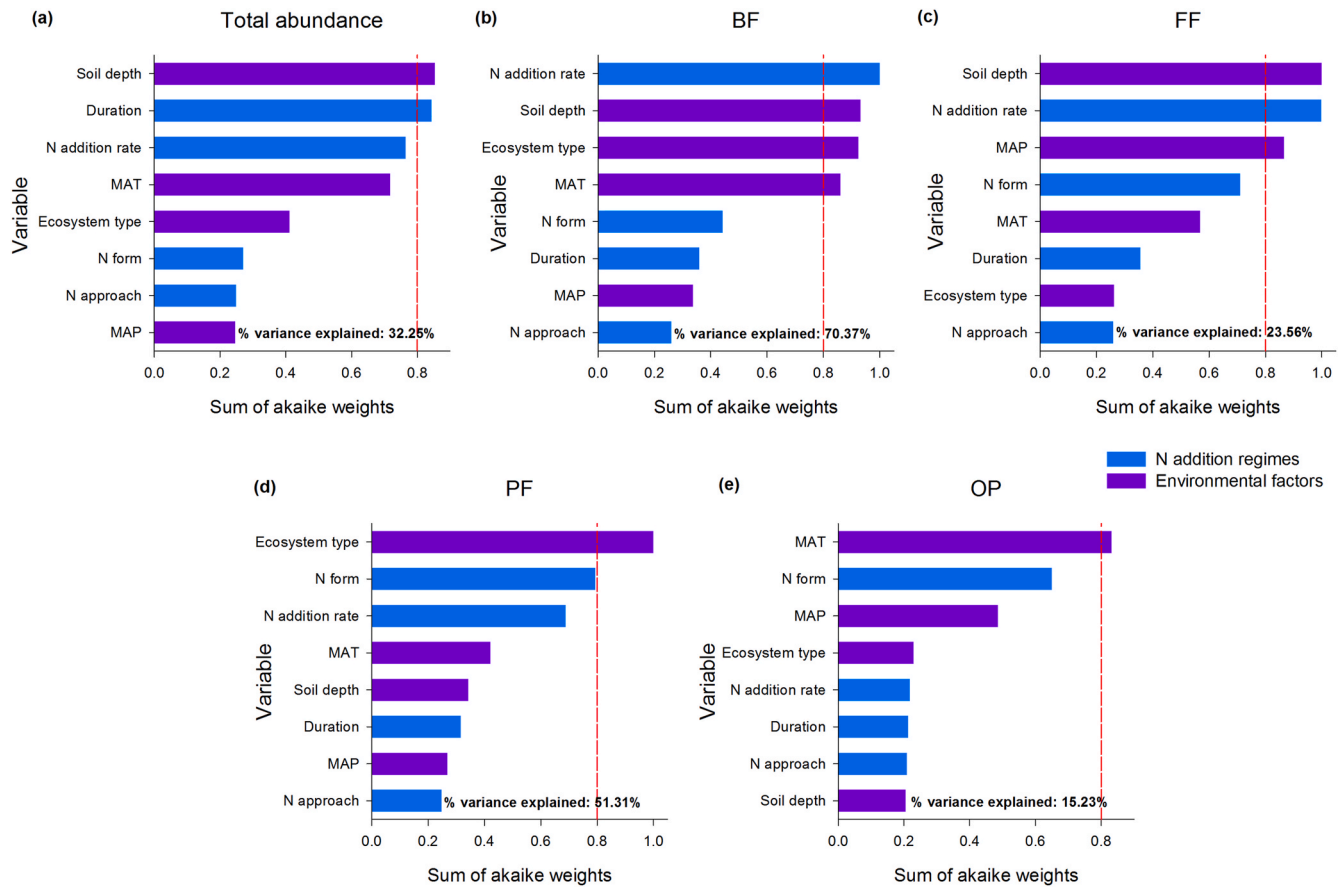

Fig. 5. Relative importance of the variables for the responses of nematode groups to N addition. Based on the sum of Akaike weights, the importance values are calculated by a model selection with corrected Akaike's information criteria. The variables include N-addition regimes (i.e., N form, application method, addition rate, and study duration) and environmental factors (i.e., latitude, longitude, biome type, soil depth, MAT, and MAP). Cutoff is set at 0.8 to estimate important and nonessential variables. MAT: mean annual temperature; MAP: mean annual precipitation.

aboveground productivity and high SOC stocks (van den Hoogen et al., 2019). Terrestrial biomes with higher biomass and biodiversity are generally more stable and resistant to environmental change and other disturbances than those with lower biomass and biodiversity (Bullock et al., 2011; Tilman et al., 2014; Isbell et al., 2015). A second possible explanation is that N is considered the nutrient most likely to limit productivity in grasslands (Xia et al., 2009). As a consequence, bacterial-feeding nematodes may be more responsive to N addition in grasslands than in forests (Bai et al., 2010; Azpilicueta et al., 2014; Shaw et al., 2019). Another notable result is that nematodes in croplands are more resistant to N addition than those in forests and grasslands. The result could be explained by the nature of croplands, which are artificial ecosystems with long-term tillage, fertilizer application, and cropping; as a consequence, nematodes in croplands may be relatively tolerant of N addition and other external disturbances.

Previous studies have reported that the addition of N could promote plant growth and soil carbon accumulation and change soil chemical parameters (Högberg et al., 2006; Tonitto et al., 2014), which would subsequently exert direct or indirect effects on nematode communities via bottom-up control or environmental stress (Liang et al., 2009; Wei et al., 2012; Chen et al., 2015). In our study, the response ratio of plant parasite index to N addition decreased as soil pH increased demonstrates that the low pH caused by N addition was conducive to plant parasite index. The possible explanation is that N addition increases the aboveground and belowground biomass of plants and provides more food sources for plant parasitic nematodes even in an acidic condition (Chen et al., 2015), resulting in the increase of the plant parasite index. However, SOC did not affect the responses of soil nematodes to N addition in our study. A meta-analysis suggested that N addition could increase aboveground litter production and the carbon content of soil organic layer, but had only marginal effects on the mineral soil layers below the organic layer (Liu and Greaver, 2010). It follows that soil depth might play critical roles in the effects of SOC on soil nematodes under N-enriched conditions. Accordingly, it was reported that the long-term N addition increased the maturity index and relative abundance of omnivorous-predatory nematodes at 0–10 cm soil depth but not at 10–20 cm soil depth in an agricultural ecosystem (Li et al., 2010). Although soil properties like soil pH and SOC may play key roles in the assemblage of nematode communities regionally, those roles were not profound in the responses of nematode communities to N addition at a global scale.

Our study indicates that temperature greatly affects the response of nematodes to N addition. The responses of total nematode abundance and the abundance of plant-feeding nematodes to N addition were positively related to mean annual temperature. Increases in temperature may increase the abundance of certain nematode trophic groups by increasing resource availability and nematode activity (Thakur et al., 2017; Ma et al., 2018). Partially consistent with our findings, previous grassland studies have found that increased temperature can enhance the abundance of bacterial-feeding nematodes (Mueller et al., 2016). Moisture also affects the responses of nematodes to N addition. A recent study found, for example, that water addition substantially reduced the abundance of bacterial-feeding nematodes in grasslands (Zhang et al., 2020), which seems inconsistent with the view that water addition usually increases plant productivity and therefore the abundances of soil organisms. Plant primary production is closely connected with nutrient

and water availability in arid and semiarid grassland ecosystems (Bai et al., 2004, 2008), and our meta-analysis indicated that the response of plant-feeding nematodes to N addition was enhanced with increasing mean annual precipitation. Water availability was also found to greatly affect nematode abundance in studies of global change (Kardol et al., 2010; Thakur et al., 2017).

Because mean annual temperature and precipitation are usually positively related at a global scale, the response ratios of soil nematodes are similar for the two factors. The abundances for all of the trophic groups of soil nematodes are considered to be higher at lower elevations with warm conditions than at higher elevations with cool conditions (Veen et al., 2017). The latter finding suggests that the response ratios of the abundance of bacterial-feeding nematodes to N addition should be positively related to mean annual temperature and precipitation, but our meta-analysis showed the opposite trend. The reason could be that bacterial-feeding nematodes, as *r*-strategists, are more likely to dominate soil nematode community in colder and drier areas as climates are getting warmer (Mueller et al., 2016). Perhaps bacterial-feeding nematodes become less responsive to N addition as mean annual temperature or precipitation increases.

5. Conclusions and future research

We conducted a meta-analysis of the effects of N addition on soil nematodes at a global scale. We found that N addition strongly affected soil nematodes and that the responses of nematode abundance to N addition are affected by both the N-addition regimes and environmental factors. We also found that offsetting effects contribute to the marginal responses of total nematode abundance, i.e., the responses of bacterial-feeding nematodes to N addition are usually positive, while the responses of other trophic groups to N addition are usually negative. We also suggest that for forest ecosystems, more studies are needed of canopy N addition so that the numbers of studies of understory N addition and canopy N addition are more balanced. Finally, we suggest that more studies on the effects of N addition on soil nematodes are needed in tropical ecosystems in order to obtain a more complete understanding of how N deposition affects soil nematodes at a global scale.

CRediT authorship contribution statement

Qingqiu Zhou: collected the data, and, and J. Wu prepared and wrote the manuscript with contributions from all the authors. **Yangzhou Xiang:** and, and. **Debao Li:** and. **Xianzhen Luo:** analyzed the data and drew the figures. **Jianping Wu:** designed and conceived of the study.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108433.

References

Aber, J., McDowell, W., Nadelhoffer, K., Magill, A., Bernston, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., Fernandez, I., 1998. Nitrogen saturation in temperate forest ecosystems. BioScience 48, 921–934.
Ackerman, D., Millet, D.B., Chen, X., 2019. Global estimates of inorganic nitrogen deposition across four decades. Global Biogeochemical Cycles 33, 100–107.
Adams, D.C., Gurevitch, J., Rosenberg, M.S., 1997. Resampling tests for meta-analysis of ecological data. Ecology 78, 1277–1283.
Azpilicueta, C.V., Aruani, M.C., Chaves, E., Reeb, P.D., 2014. Soil nematode responses to fertilization with ammonium nitrate after six years of unfertilized apple orchard. Spanish Journal of Agricultural Research 12, 353–363.
Bai, Y., Han, X., Wu, J., Chen, Z., Li, L., 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431, 181–184.
Bai, Y., Wu, J., Clark, C.M., Naeem, S., Pan, Q., Huang, J., Zhang, L., Han, X., 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. Global Change Biology 16, 358–372.
Bai, Y., Wu, J., Xing, Q., Pan, Q., Huang, J., Yang, D., Han, X., 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia Plateau. Ecology 89, 2140–2153.
Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Applied Soil Ecology 10, 239–251.
Bongers, T., van der Meulen, H., Korthals, G., 1997. Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions. Applied Soil Ecology 6, 195–199.
Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in Ecology & Evolution 26, 541–549.
Chen, D., Lan, Z., Hu, S., Bai, Y., 2015. Effects of nitrogen enrichment on belowground communities in grassland: relative role of soil nitrogen availability vs. soil acidification. Soil Biology and Biochemistry 89, 99–108.
Chen, D., Zheng, S., Shan, Y., Taube, F., Bai, Y., 2013. Vertebrate herbivore-induced changes in plants and soils: linkages to ecosystem functioning in a semi-arid steppe. Functional Ecology 27, 273–281.
Chen, J., Elsgaard, L., van Groenigen, K.J., Olesen, J.E., Liang, Z., Jiang, Y., Lærke, P.E., Zhang, Y., Luo, Y., Hungate, B.A., Sinsabaugh, R.L., Jørgensen, U., 2020. Soil carbon loss with warming: new evidence from carbon-degrading enzymes. Global Change Biology 26, 1944–1952.
Chen, J., Luo, Y., Garcia-Palacios, P., Cao, J., Dacal, M., Zhou, X., Li, J., Xia, J., Niu, S., Yang, H., Shelton, S., Guo, W., van Groenigen, K.J., 2018. Differential responses of carbon-degrading enzyme activities to warming: implications for soil respiration. Global Change Biology 24, 4816–4826.
Collyer, M.L., Adams, D.C., Freckleton, R., 2018. RRPP: an r package for fitting linear models to high-dimensional data using residual randomization. Methods in Ecology and Evolution 9, 1772–1779.
Crowther, T.W., Boddy, L., Jones, T.H., 2011. Species-specific effects of soil fauna on fungal foraging and decomposition. Oecologia 167, 535–545.
Ferris, H., 2010. Contribution of nematodes to the structure and function of the soil food web. Journal of Nematology 42, 63–67.
Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18, 13–29.
Forge, T.A., Bittman, S., Kowalenko, C.G., 2005. Responses of grassland soil nematodes and protozoa to multi-year and single-year applications of dairy manure slurry and fertilizer. Soil Biology and Biochemistry 37, 1751–1762.
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.
Gruzdeva, L.I., Matveeva, E.M., Kovalenko, T.E., 2007. Changes in soil nematode communities under the impact of fertilizers. Eurasian Soil Science 40, 681–693.
Högberg, P., Fan, H., Quist, M., Binkley, D.A.N., Tamm, C.O., 2006. Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. Global Change Biology 12, 489–499.
Hu, C., Qi, Y., 2010. Effect of compost and chemical fertilizer on soil nematode community in a Chinese maize field. European Journal of Soil Biology 46, 230–236.
Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–589.
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.
Leff, J.W., Jones, S.E., Prober, S.M., Barberan, A., Borer, E.T., Firn, J.L., Harpole, W.S., Hobbie, S.E., Hofmockel, K.S., Knops, J.M., McCulley, R.L., La Pierre, K., Risch, A.C., Seabloom, E.W., Schutz, M., Steenbock, C., Stevens, C.J., Fierer, N., 2015. Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. Proceedings of the National Academy of Sciences of the United States of America 112, 10967–10972.
Li, Q., Jiang, Y., Liang, W., Lou, Y., Zhang, E., Liang, C., 2010. Long-term effect of fertility management on the soil nematode community in vegetable production under greenhouse conditions. Applied Soil Ecology 46, 111–118.

Liang, W., Lou, Y., Li, Q., Zhong, S., Zhang, X., Wang, J., 2009. Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in Northeast China. Soil Biology and Biochemistry 41, 883–890.
Liu, L., Greaver, T.L., 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. Ecology Letters 13, 819–828.
Liu, T., Chen, X., Hu, F., Ran, W., Shen, Q., Li, H., Whalen, J.K., 2016a. Carbon-rich organic fertilizers to increase soil biodiversity: evidence from a meta-analysis of nematode communities. Agriculture, Ecosystems & Environment 232, 199–207.
Liu, T., Mao, P., Shi, L., Eisenhauer, N., Liu, S., Wang, X., He, X., Wang, Z., Zhang, W., Liu, Z., Zhou, L., Shao, Y., Fu, S., 2020. Forest canopy maintains the soil community composition under elevated nitrogen deposition. Soil Biology and Biochemistry 143, 107733.
Liu, T., Whalen, J.K., Ran, W., Shen, Q., Li, H., 2016b. Bottom-up control of fertilization on soil nematode communities differs between crop management regimes. Soil Biology and Biochemistry 95, 198–201.
Lokupitiya, E., Stanton, N.L., Seville, R.S., Snider, J.R., 2000. Effects of increased nitrogen deposition on soil nematodes in alpine tundra soils. Pedobiologia 44, 591–608.
Lu, X., Vitousek, P.M., Mao, Q., Gilliam, F.S., Luo, Y., Zhou, G., Zou, X., Bai, E., Scanlon, T.M., Hou, E., Mo, J., 2018. Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest. Proceedings of the National Academy of Sciences of the United States of America 115, 5187–5192.
Ma, Q., Yu, H., Liu, X., Xu, Z., Zhou, G., Shi, Y., 2018. Climatic warming shifts the soil nematode community in a desert steppe. Climatic Change 150, 243–258.
Mao, Q., Lu, X., Zhou, K., Chen, H., Zhu, X., Mori, T., Mo, J., 2017. Effects of long-term nitrogen and phosphorus additions on soil acidification in an N-rich tropical forest. Geoderma 285, 57–63.
Mueller, K.E., Blumenthal, D.M., Carrillo, Y., Cesarz, S., Ciobanu, M., Hines, J., Pabst, S., Pendall, E., de Tomasel, C.M., Wall, D.H., Eisenhauer, N., 2016. Elevated CO_2 and warming shift the functional composition of soil nematode communities in a semiarid grassland. Soil Biology and Biochemistry 103, 46–51.
Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. Journal of Nematology 33, 161–168.
Neher, D.A., Weicht, T.R., Barbercheck, M.E., 2012. Linking invertebrate communities to decomposition rate and nitrogen availability in pine forest soils. Applied Soil Ecology 54, 14–23.
Pan, K., Gong, P., Wang, J., Wang, Y., Liu, C., Li, W., Zhang, L., 2015. Applications of nitrate and ammonium fertilizers alter soil nematode food webs in a continuous cucumber cropping system in Southwestern Sichuan, China. Eurasian Journal of Soil Science 4, 287–300.
Pan, K., Xu, Z., Blumfield, T., Totua, S., Lu, M., 2008. In situ mineral ^{15}N dynamics and fate of added $^{15}NH_4^+$ in hoop pine plantation and adjacent native forest in subtropical Australia. Journal of Soils and Sediments 8, 398–405.
Peng, Y., Chen, G., Chen, G., Li, S., Peng, T., Qiu, X., Luo, J., Yang, S., Hu, T., Hu, H., Xu, Z., Liu, L., Tang, Y., Tu, L., 2017. Soil biochemical responses to nitrogen addition in a secondary evergreen broad-leaved forest ecosystem. Scientific Reports 7, 2783.
Pittelkow, C.M., Liang, X., Linquist, B.A., van Groenigen, K.J., Lee, J., Lundy, M.E., van Gestel, N., Six, J., Venterea, R.T., van Kessel, C., 2015. Productivity limits and potentials of the principles of conservation agriculture. Nature 517, 365–368.
Shao, Y., Zhang, W., Eisenhauer, N., Liu, T., Xiong, Y., Liang, C., Fu, S., 2017. Nitrogen deposition cancels out exotic earthworm effects on plant-feeding nematode communities. Journal of Animal Ecology 86, 708–717.
Shaw, E.A., Boot, C.M., Moore, J.C., Wall, D.H., Baron, J.S., 2019. Long-term nitrogen addition shifts the soil nematode community to bacterivore-dominated and reduces its ecological maturity in a subalpine forest. Soil Biology and Biochemistry 130, 177–184.
Thakur, M.P., Tilman, D., Purschke, O., Ciobanu, M., Cowles, J., Isbell, F., Wragg, P.D., Eisenhauer, N., 2017. Climate warming promotes species diversity, but with greater taxonomic redundancy, in complex environments. Science advances 3, e1700866.
Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annual Review of Ecology Evolution and Systematics 45, 471–493.
Tonitto, C., Goodale, C.L., Weiss, M.S., Frey, S.D., Ollinger, S.V., 2014. The effect of nitrogen addition on soil organic matter dynamics: a model analysis of the Harvard Forest Chronic Nitrogen Amendment Study and soil carbon response to anthropogenic N deposition. Biogeochemistry 117, 431–454.
Treonis, A.M., Unangst, S.K., Kepler, R.M., Buyer, J.S., Cavigelli, M.A., Mirsky, S.B., Maul, J.E., 2018. Characterization of soil nematode communities in three cropping systems through morphological and DNA metabarcoding approaches. Scientific Reports 8, 2004.
Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. Ecology Letters 11, 1111–1120.
van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martín, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T. O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J.-i., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198.
Veen, G.F., De Long, J.R., Kardol, P., Sundqvist, M.K., Snoek, L.B., Wardle, D.A., 2017. Coordinated responses of soil communities to elevation in three subarctic vegetation types. Oikos 126, 1586–1599.
Wang, S., Cai, M., Li, D., Wu, B., Li, J., Huang, G., Duan, H., Wu, J., 2021. Heat waves intensify the effects of drought on bacterial diversity but not community composition in *Solanum lycopersicum* soil. Journal of Soils and Sediments 21, 355–363.
Wei, C., Zheng, H., Li, Q., Lü, X., Yu, Q., Zhang, H., Chen, Q., He, N., Kardol, P., Liang, W., Han, X., 2012. Nitrogen addition regulates soil nematode community composition through ammonium suppression. PloS One 7, e43384.
Wu, J., Liu, W., Fan, H., Huang, G., Wan, S., Yuan, Y., Ji, C., 2013. Asynchronous responses of soil microbial community and understory plant community to simulated nitrogen deposition in a subtropical forest. Ecology and Evolution 3, 3895–3905.
Xia, J., Niu, S., Wan, S., 2009. Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe. Global Change Biology 15, 1544–1556.
Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. Agriculture, Ecosystems & Environment 74, 113–135.
Yu, G., Jia, Y., He, N., Zhu, J., Chen, Z., Wang, Q., Piao, S., Liu, X., He, H., Guo, X., Wen, Z., Li, P., Ding, G., Goulding, K., 2019. Stabilization of atmospheric nitrogen deposition in China over the past decade. Nature Geoscience 12, 424–429.
Zhang, G., Sui, X., Li, Y., Jia, M., Wang, Z., Han, G., Wang, L., 2020. The response of soil nematode fauna to climate drying and warming in *Stipa breviflora* desert steppe in Inner Mongolia, China. Journal of Soils and Sediments 20, 2166–2180.
Zhang, X., Jiang, Y., Liang, L., Zhao, X., Li, Q., 2009. Response of soil nematode communities to long-term application of inorganic fertilizers in the black soil of Northeast China. Frontiers of Biology in China 4, 111–116.
Zhao, J., Neher, D.A., Fu, S., Li, Z., Wang, K., 2013. Non-target effects of herbicides on soil nematode assemblages. Pest Managemant Science 69, 679–684.
Zhao, J., Wang, F., Li, J., Zou, B., Wang, X., Li, Z., Fu, S., 2014. Effects of experimental nitrogen and/or phosphorus additions on soil nematode communities in a secondary tropical forest. Soil Biology and Biochemistry 75, 1–10.
Zhou, Q., Li, J., Wang, S., Wu, B., Chen, H., Deng, Y., Wu, J., 2020. Short-term effects of warming and nematodes addition on soil respiration of Xishuangbanna tropical rainforest. Ecology and Environmental Sciences 29, 1752–1758.