



Systematic review and meta-analysis

Mechanisms underlying the negative effects of nitrogen addition on soil nematode communities in global grassland ecosystems

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ABSTRACT

Reactive nitrogen (N) can significantly influence the richness and abundance of a myriad of organisms; however, it remains unclear how the addition of N affects soil nematodes and their associated ecosystem functions in natural grasslands on a global scale. For this study, we synthesized data on the responses of soil nematode taxon richness and abundance to N addition based on 72 published papers that investigated different grassland ecosystems. Subsequently, we explored the potential mechanisms that underlie the impacts of N addition on soil nematode communities. We found that N addition generally reduced the total nematode taxon richness and abundance of fungal-feeding and omnivorous-carnivorous nematodes in grasslands worldwide. These negative effects of N enrichment on nematodes primarily existed in temperate grassland and meadows, which were influenced through the addition of ammonium nitrate, and became stronger with higher rates of N addition. Further, our structural equation model revealed that the rate of N addition reduced the total nematode taxon richness and abundances of multiple trophic groups (e.g., plant-feeding, bacterial-feeding, fungal-feeding, and omnivorous-carnivorous nematodes) by increasing soil ammonium concentrations and by decreasing microbial biomass carbon, despite the influence of N on plant biomass promoting nematode richness and abundances. In addition, higher soil acidification following the increased N addition rate, directly and indirectly reduced nematode taxon richness and the abundance of different nematode groups, by decreasing plant biomass and microbial biomass carbon. In terms of ecosystem functionality, the negative impacts of N addition on soil nematodes were found to be closely linked with the reduced soil carbon mineralization rate. Taken together, our results suggested that N enrichment negatively impacted the taxon richness and abundance of nematode communities and their associated soil carbon mineralization across global grassland ecosystems. Earth system models that predict belowground communities and linkages to carbon cycling should consider the increases in soil ammonium concentrations and soil acidification under future scenarios of N deposition.

1. Introduction

Anthropogenic inputs of reactive nitrogen (N), originating mainly from industrial fuel use and agricultural fertilization, have increased three-to-five-fold over the last century (Ackerman et al., 2019; Galloway et al., 2008). Increased N inputs to grassland ecosystems strongly regulate the diversity and composition of both plant and microbial communities (Bai et al., 2010; Treseder, 2008; Zhang et al., 2018). However, soil nematodes, including plant-feeding (PF), bacterial-feeding (BF), fungal-feeding (FF), and omnivorous-carnivorous (OC)

feeding-groups, have been shown to be sensitive to the increased availability of soil N in grasslands (Peng et al., 2022; Wardle et al., 2013; Xing et al., 2022). As widespread and diverse fauna groups in grasslands (Bardgett and Chan, 1999; Bardgett et al., 1999), soil nematodes have potential effects on soil carbon (C) and nutrient cycling (Ferris, 2010; Ferris et al., 1997; Ingham et al., 1985). Many earlier studies examined the effects of N addition on nematode communities in grasslands at the local scale, with great variations in the direction and magnitude of responses to N enrichment across different studies (Chen et al., 2015a; Song et al., 2016; Treseder, 2008). Considering that 69% of the globe's

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agriculture is pasture (Food and Agriculture Organization of the United Nations), a better understanding of the mechanisms that underly the responses of soil nematodes to N enrichment across global grasslands is important for regulating the fertilization management in pasture systems.

Previous studies have shown that effects of N enrichment on the richness and abundance of soil nematode communities can be either positive (Hu et al., 2017), negative (Wei et al., 2012), or neutral (Siebert et al., 2019). These inconsistencies likely resulted from different grassland ecosystem types, N forms, N addition rates, and experimental durations. Firstly, abundance of nematodes tends to increase in desert (Alon and Steinberger, 1999), but decrease in temperate grassland and meadow under N enrichment (Chen et al., 2019). This is likely due to nutrient deficiencies in the desert, which constrain the growth of nematodes in contrast to temperate grassland and meadow (Tian et al., 2016). Secondly, the addition of ammonium nitrate (NH_4NO_3) typically has detrimental effects on the richness and abundance of nematode communities, as increased NH_4^+ concentrations and induced soil acidification often restrict the growth of PF, FF, and OC nematodes (Chen et al., 2015a; Song et al., 2016; Treseder, 2008). However, the application of organic urea may be of benefit to some soil nematodes (e.g., FF nematodes); thus, stimulating their diversity by increasing microbial food source such as fungal biomass (Wang et al., 2018). Thirdly, small N inputs in grasslands may stimulate the growth of PF and free-living (BF, FF, and OC) nematodes by increasing plant root exudates or microbial biomass carbon (MBC) (Cesarz et al., 2015). Conversely, excessive N inputs may strongly reduce nematode taxon richness and abundance by overwhelming their N demands (Chen et al., 2015a; Chen et al., 2019). Finally, the positive responses of soil nematode richness and abundance to N addition might transition to negative, or negative responses may be amplified with prolonged experiments as the result of cumulative toxic effects and deterioration of nematode living conditions (Tian and Niu, 2015; Tian et al., 2016).

Changes in soil abiotic factors can mediate the impacts of N addition on nematode richness and abundance. Specifically, N enrichment can decrease nematode richness and abundance by increasing soil NH_4^+ concentrations and/or by decreasing the soil pH. Under N addition, increased soil NH_4^+ can be absorbed by many plant species to ultimately accumulate in their root systems (Wall and Tiedjens, 1940). When plant feeding (PF) nematodes parasitize roots and ingest NH_4^+ rich cell fluids and exudates for their growth, NH_4^+ poisoning may be induced (Kronzucker et al., 2001; Wei et al., 2012). Compared with PF nematodes, increased soil NH_4^+ concentrations can also inhibit the growth and abundance of omnivorous and carnivorous (OC) nematodes, which is likely due to their weaker osmoregulatory capacities, with less developed cuticle structures and secretory-excretory systems (Tenuta and Ferris, 2004). Furthermore, soil acidification caused by N addition can modify nematode living conditions by releasing soil H^+ and/or by mobilizing metal ions, which have potent toxic effects on nematode richness and abundance. Alternatively, the low concentrations of base cations (e.g., Na^+ , Mg^{2+} , and Ca^{2+}) under soil acidification might induce nutrient deficiencies in nematodes, resulting in the low diversity and abundance of their communities (Chen et al., 2015a; Chen et al., 2015b; Tian and Niu, 2015).

Additionally, N enrichment may indirectly affect nematode taxon richness and abundance through its strong effects on plant and microbial communities (Keith et al., 2009; Pollierer et al., 2007). The higher availability of soil N generally increases aboveground biomass (AGB) of plants, and thus their root biomass, which promotes the richness and abundance of PF nematodes by supplying them with abundant quantities of nutrients (Keith et al., 2009). Increased carbon inputs from roots can also alleviate C limitations for microbial communities and stimulate the generation of microbial biomass, which facilitates the growth of free-living nematodes (e.g., BF and FF) that feed on microbes (Wang et al., 2022). On the other hand, the increased availability of N can stimulate the generation of microbial biomass by alleviating microbial nutrient

limitations (Zhou et al., 2017), with the strong bottom-up effects of food resources on free-living nematodes. In contrast, excessive N inputs may induce soil acidification, which imposes strong physiological constraints on both plants and microorganisms; thus, decoupling their relationships with nematodes (Chen et al., 2015a; Xiao et al., 2020). Despite changes in multiple abiotic and biotic factors under the addition of N, which might have significant impacts on nematode communities, it remains unknown what the key drivers of soil nematode richness and abundance are in response to N enrichment in various grassland ecosystems.

The feeding modes of different nematode groups are important in controlling microbial-mediated processes such as soil C mineralization (Bardgett et al., 1999; Thakur and Geisen, 2019). For instance, PF nematodes can infect the roots of many plant species, which induce the leakage of carbohydrates and nutrients from injured roots; thus, increasing food supplies for microbial communities and accelerating C cycling in the rhizosphere soil (Gan and Wickings, 2020; Yeates et al., 1999; Yeates et al., 1998). In addition, BF and FF nematodes primarily feed on bacteria and fungi, respectively, which accelerates the growth and metabolism of microbes and promotes the C mineralization rate (Alkemade et al., 1992; Ingham et al., 1985; Trofymow and Coleman, 2021; Wu et al., 2007). However, the predation of OC nematodes on BF and FF nematodes can suppress the growth and reproduction of free-living nematodes. These effects can cascade down to the base of the soil micro-food web, to ultimately decrease the microbial biomass and soil C mineralization rate (Allen-Morley and Coleman, 1989; Hedlund and Öhrn, 2000; Wardle et al., 1995). Therefore, it is expected that the effects of nematodes on microbes, and thus on soil C mineralization are contingent on the specific feeding habits of nematode trophic groups (Bardgett and Cook, 1998; De Mesel et al., 2004; Fu et al., 2005). Considering that increased quantities of reactive N strongly regulate the richness and abundance of different nematode trophic groups, it may be anticipated that its addition might alter the diversity and composition of soil nematode communities, which in turn will affect the soil C mineralization rate across grasslands worldwide.

To explore the mechanisms that underly the richness, abundance, and composition of nematode communities in response to N enrichment across different grassland ecosystems, we compiled 72 published peer-reviewed papers with 55 field sites that encompassed most grassland ecosystem types, with a focus on the effects of N addition on nematode communities (Appendices S1, S2). A meta-analysis approach was employed to answer the following questions: (1) How are nematode taxon richness and abundance affected by the addition of N (e.g., N forms, N addition rates, and experimental durations) across global grassland ecosystems? (2) What are the mechanisms that underly the impacts of N addition on the richness, abundance, and composition of nematode communities? (3) How are the responses of richness and abundance to N addition linked to changes in the soil C mineralization rate?

2. Materials and methods

2.1. Data preparation

The data for this study were collected by surveying published peer-reviewed articles on the theme of N addition experiments and soil nematode taxon richness and abundance. Searched databases included Google Scholar, Web of Science, and the China National Knowledge Infrastructure Database, up to 1 September 2022. The keywords used for the online literature search included, “nitrogen addition/ nitrogen application/ nitrogen deposition/ nitrogen enrichment/ nitrogen fertilization/ nitrogen input/ nitrogen amendment” and “nematod*/ fungivor*/ bacterivor*/ omnivor*/ predat*/ carnivor*/ nematode community/ nematode feeding groups/ plant-feeding nematode/ bacterial-feeding nematode/ fungal-feeding nematode/ omnivorous nematode/ carnivorous nematode”. The following criteria were employed to select the appropriate studies. (1) Only field experiments in grassland ecosystems were included. (2) N addition and

control treatment plots shared the same conditions, such as climate, vegetation, and soil type. (3) Types of N fertilizer, N addition rates, and experimental durations were clearly reported. (4) At least one index among nematode taxon richness or total nematode abundance, and abundances of different trophic groups (PF, BF, FF, and OC) was reported. (5) Response variables were explicitly provided with their means and sample sizes.

The data were directly copied from texts and tables or digitized from figures using Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA). For each study, we collected the N fertilizer type, N addition rate ($\text{g N m}^{-2} \text{ year}^{-1}$), experimental duration (years), nematode taxon richness, total nematode abundance, and the abundance of PF, BF, FF, and OC nematodes (Table S1). As most studies reported the number of genera as an indicator of nematode richness, we consistently collected the genus diversity of nematode communities. The nematode abundance (individuals per 100 g dry soil) was reported and collected at the community and trophic group levels. Environmental factor data were also collected, which were closely related to nematode communities (e.g., soil N availability (NH_4^+ and NO_3^-), soil pH, AGB, MBC, and soil C mineralization rate). As most of our collected studies reported that the soil C mineralization rate was measured via aerobic incubation procedure in the laboratory (Chen et al., 2019; van Eekeren et al., 2009), we thus consistently collected the C mineralization data based on lab incubation method. Overall, 55 independent grassland study sites from 72 papers met the criteria described above (Note S1, Table S1). Specifically, we condensed the reported grasslands into five groups based on their distinct vegetation types following the protocol of Wang et al. (2019) and Zhang (2007): temperate grassland and meadow, alpine grassland and meadow, desert, savanna, and tundra (Appendices S1, S2). The fertilizer types used in the selected studies were NH_4NO_3 , other ammonium salts, other nitrate salts, and urea. Other ammonium salts included $(\text{NH}_4)_2\text{HPO}_4$ or $(\text{NH}_4)_2\text{SO}_4$. Other nitrate salts included KNO_3 . The N addition rate ranged from 0.1 to $84 \text{ g N m}^{-2} \text{ year}^{-1}$, and the experimental duration ranged from 1 to 27 years. The mean annual temperature ranged from -12.5°C to 28.2°C and the mean annual precipitation ranged from 80 to 1744 mm.

2.2. Statistical analyses

Firstly, the natural log-transformed response ratio (lnRR) was used to calculate the effects of the experimental treatments for all response variables (Hedges et al., 1999): $\ln\text{RR} = \ln(\bar{X}_t / \bar{X}_c)$, where $\bar{X}_t$ and $\bar{X}_c$ were the mean values of response variables in the N addition and control plots, respectively. Estimates of effect sizes and subsequent inferences are generally dependent on how individual observations are weighted. Weighting functions based on sampling variance may assign extreme importance to a few individual observations, which might lead to the lnRR being primarily determined by a few studies (Ma and Chen, 2016). Further, in our dataset, we found that 24 of 72 studies did not report the sampling variance. Based on the above considerations, we calculated the weighting factors (w) with the sample size of response variables (Adams et al., 1997), $w = N_t \times N_c / (N_t + N_c)$, where N_t and N_c represent the number of replications for the N addition and control treatments, respectively.

Second, the linear mixed effect model was employed to analyze the mean N addition effects on each response variable, as well as their corresponding 95% confidence intervals (CIs). For these models, ecosystem types (temperate grassland and meadow, alpine grassland and meadow, desert, savanna, and tundra), fertilizer types (NH_4NO_3 , other ammonium salts, other nitrate salts, and urea), N addition rates (<5 , 5–10, 10–15, and $>15 \text{ g N m}^{-2} \text{ year}^{-1}$), and experimental durations (<5 , 5–10, 10–15, and >15 years) were treated as fixed effects, and the study sites were treated as random intercepts to handle the potential autocorrelations between observations in each study. If the 95% CI did not cover zero, the effect of N addition on the response

variable was considered significant. For convenience and clarification, the lnRR and its corresponding CI were transformed back to the percentage change as $(e^{\ln\text{RR}} - 1) \times 100\%$. We also used linear mixed effect models to examine how the addition of N induced changes in abiotic and biotic factors and influenced soil nematodes.

Third, we applied piecewise structural equation modelling (piecewise SEM) (Lefcheck, 2016) to test the relationships between the N addition rate, experimental duration, lnRRs of abiotic soil factors (NH_4^+ , NO_3^- , pH), lnRRs of biotic factors (AGB and MBC), and lnRRs of nematode variables (taxon richness, abundance, and composition of nematode communities). There were 59 observations in SEM, which covered a large range of N addition rates (1.5 to $30 \text{ g N m}^{-2} \text{ year}^{-1}$) and experimental durations (1 to 16 years). Piecewise SEM allowed for the development and testing of highly complex causal models using comparatively low sample sizes (exceeded the total observations or sample size $n = 40$) (Lefcheck, 2016). Based on the hypothesized mechanisms, we developed an a priori conceptual model that depicted the causal relationships between these variables in a path diagram (Appendix S3). The conceptual SEM contained: 1) the direct pathways of abiotic soil factors (lnRRs of soil NH_4^+ , NO_3^- , and pH) on nematode variables (lnRRs of total nematode taxon richness and abundance, and lnRRs of PF, BF, FF, and OC abundance) under N addition, and 2) the indirect pathways of abiotic soil factors on nematode variables via changes in the lnRRs of AGB and MBC. Because the lnRRs of different nematode abundances were often correlated, we used principal component analysis (PCA) to create multivariate indices for the lnRRs of PF, BF, FF, and OC abundances (Chen et al., 2015a; Chen et al., 2015b) (Appendix S4). The PCA revealed that the first principal component (PC1) alone explained 71% of the total variance of the lnRRs of PF, BF, FF, and OC nematode abundances, which was used as indicator of nematode community composition in response to N addition. In particular, all the lnRRs of PF, BF, FF, and OC abundances had negative loadings on the PC1 axis. Thus, PC1 represented a gradient of study sites from those with high lnRRs of nematode abundances of four trophic groups at the PC1 negative axis to those with the low lnRRs of nematode abundances for the four trophic groups at the PC1 positive axis (Appendix S4). The component models of piecewise SEM were fitted as linear mixed models, with the abiotic and biotic factors as fixed effects, studies as random effect, and sites nested in the study as an error term. The N addition rate and experimental duration were transformed to natural logarithms prior to piecewise SEM analysis to mitigate the departure from normality and linearity. The overall goodness of model fit was evaluated using Akaike information criterion (AIC) (the lowest AIC value indicated the best model), Chi-square distributed Fisher's C statistic (the lowest Fisher's C value indicated the best model), and its associated P value ($P > 0.05$ indicated an adequate model fit) (Grace, 2006; Lefcheck, 2016).

Finally, partial regressions were employed to graphically demonstrate how the effects of N addition on the lnRR of soil $C_{\min}$ changed with nematode variables after controlling for the effects of N addition on the lnRR of MBC. Briefly, we analyzed these relationships following the modelling equation: $\ln\text{RR of } C_{\min} = \beta_0 + \beta_1 \times \ln\text{RR of nematode variables} + \beta_2 \times \ln\text{RR of MBC} + \pi_{\text{site}} + \varepsilon$, where β , π_{site} , and ε are the coefficient, the site random effect factor, and the sampling error, respectively. Partial residual estimates were obtained that were not explained by the lnRR of MBC, using the residuals from the above modelling equation plus the mean intercept coefficient β_0 , plus the coefficient β_1 multiplied by nematode variables, following the method described by Chen et al. (2021).

All data analyses were performed using R software (version 4.0.4; R Development Core Team, 2021) with the *lme4* and *piecewiseSEM* packages (Bates et al., 2015; Lefcheck, 2016).

3. Results

3.1. Effects of N addition on soil nematode taxon richness and abundance

The addition of N significantly reduced the soil nematode total taxon richness, and the abundances of FF and OC nematodes, while it did not affect the total nematode abundance, and abundances of PF and BF nematodes (Figs. 1, 2). Among the different grassland ecosystems, the addition of N reduced the nematode taxon richness, total abundance, and abundances of PF, FF, and OC groups in temperate grassland and meadow (Figs. 1, 2). The addition of N had no impacts on nematode variables in alpine grassland and meadow, desert, and savanna. It significantly increased the abundance of the BF group in alpine grassland and meadow, and tundra, and increased the abundance of the FF group in tundra (Fig. 2).

The addition of NH_4NO_3 decreased the nematode taxon richness and abundances of the PF, FF, and OC groups; however, the addition of other ammonium salts increased the abundance of the BF group only, while the addition of urea decreased the abundance of only the OC group (Figs. 1, 2). When the N addition rate was $< 5 \text{ g m}^{-2} \text{ year}^{-1}$, the N addition did not affect the nematode taxon richness and abundances (Figs. 1, 2). When the N addition rate was $5\text{--}10 \text{ g m}^{-2} \text{ year}^{-1}$, the N addition significantly decreased nematode taxon richness and OC abundance but increased the BF abundance (Figs. 1, 2). When the N addition rate was $10\text{--}15 \text{ g m}^{-2} \text{ year}^{-1}$, the N addition significantly increased the BF abundance and decreased the OC abundance (Figs. 1, 2). When the N addition rate was $> 15 \text{ g m}^{-2} \text{ year}^{-1}$, the N addition significantly decreased the nematode taxon richness and abundance of the total, PF, BF, FF, and OC nematodes. For different experimental durations, the N addition significantly reduced the abundances of FF and OC with durations of less than five years (Fig. 2). The N addition significantly reduced nematode richness, total abundances, and abundances of PF, FF, and OC nematodes with durations of 5–10 years (Figs. 1, 2). Furthermore, negative OC abundance responses were greater under prolonged experiments (Fig. 2).

3.2. Multivariate relationships between responses of soil nematode variables and soil abiotic and biotic factors under N addition

Our linear mixed effect models revealed that N addition significantly

increased the concentrations of the soil NO_3^- and NH_4^+ , and AGB, but decreased the soil pH (Appendix S5). In addition, the increased $\ln\text{RR}$ of NH_4^+ was negatively related with the $\ln\text{RR}$ s of PF, BF, FF, and OC abundances, while the decreased $\ln\text{RR}$ of pH was positively associated with responses of these nematode variables (Appendix S6).

The SEM further indicated that the N addition rate directly increased the $\ln\text{RR}$ s of the NO_3^- concentration ($r = 0.71$), NH_4^+ concentration ($r = 0.53$), and AGB ($r = 0.49$), but decreased the $\ln\text{RR}$ s of the soil pH ($r = -0.29$) and MBC ($r = -0.37$) (Fig. 3). However, the experimental duration had no effect on the abovementioned variables. Further, the $\ln\text{RR}$ of the NH_4^+ concentration had a direct negative effect on the $\ln\text{RR}$ of total taxon richness ($r = -0.28$). The $\ln\text{RR}$ of the NH_4^+ concentration also had a direct negative effect on the PC1 ($r = -0.26$), which suggested that increases in the NH_4^+ concentration decreased the $\ln\text{RR}$ s of PF, BF, FF, and OC nematode abundances. Moreover, the $\ln\text{RR}$ of the NH_4^+ concentration indirectly increased the $\ln\text{RR}$ s of nematode taxon richness, total abundance, and PC1 by promoting the $\ln\text{RR}$ s of AGB and MBC.

The SEM also showed that the N addition rate had a direct negative effect on the $\ln\text{RR}$ of the soil pH ($r = -0.29$), where the $\ln\text{RR}$ of the soil pH had a direct positive effect on the PC1 ($r = 0.34$), suggesting that the N addition rate could reduce the $\ln\text{RR}$ s of PF, BF, FF, and OC abundances by reducing the soil pH. Additionally, the decreased $\ln\text{RR}$ of the soil pH indirectly reduced the $\ln\text{RR}$ s of the nematode taxon richness, total abundance, and PC1 via changes in the $\ln\text{RR}$ s of AGB ($r = 0.39$) and MBC ($r = 0.18$). Ultimately, under N addition, the total taxon richness and abundances were decreased (on average) by 10% and 27%, while the abundances of PF, BF, FF, and OC nematodes were decreased (on average) by 20%, 12%, 42%, and 55%, respectively.

3.3. Relationships of the responses of nematode richness and abundance with the C mineralization rate

After controlling the effects of the $\ln\text{RR}$ of MBC on the $\ln\text{RR}$ of soil C mineralization under N addition, partial regression analysis showed that the $\ln\text{RR}$ of the C mineralization rate was positively related to the $\ln\text{RR}$ s of the nematode total taxon richness, total abundance, and the abundances of PF and FF groups, while it had no relationship with the $\ln\text{RR}$ of BF and OC abundances (Fig. 4).

4. Discussion

4.1. Effects of N addition on soil nematode taxon richness

We found that the addition of N significantly reduced the nematode total taxon richness across grassland ecosystems, which was consistent with our first hypothesis and previous findings, where N enrichment constrained nematode diversity in grasslands (Chen et al., 2015a; Eisenhauer et al., 2012; Song, 2017; Wei et al., 2012). However, the negative responses of nematode taxon richness to N addition dominated in temperate grassland and meadow but not in alpine grassland and meadow, desert, and tundra. In our dataset, the extensive research in temperate grassland and meadow indicated that soil acidification and ammonium toxicity were more severe under the addition of NH_4NO_3 , with strong negative effects on nematode taxon richness and abundance. In contrast, the limited number of studies conducted in alpine grassland and meadow, desert, and tundra could largely prevent the detection of the general trends of nematode richness responses to N addition.

We found that N-induced nematode taxon richness loss became dramatic when the N addition rate was $> 15 \text{ g N m}^{-2} \text{ year}^{-1}$. One possible reason was that the accumulation of soil H^+ , Al^{3+} , and NH_4^+ under high N addition rates prohibited the growth and proliferation of diverse nematode groups, thereby reducing nematode richness (Chen et al., 2019; Nagy, 1999; Warren, 1962; Xing et al., 2022). We also found that N addition over 5–10 years had a negative impact on nematode richness. This result was consistent with a short-term study conducted in

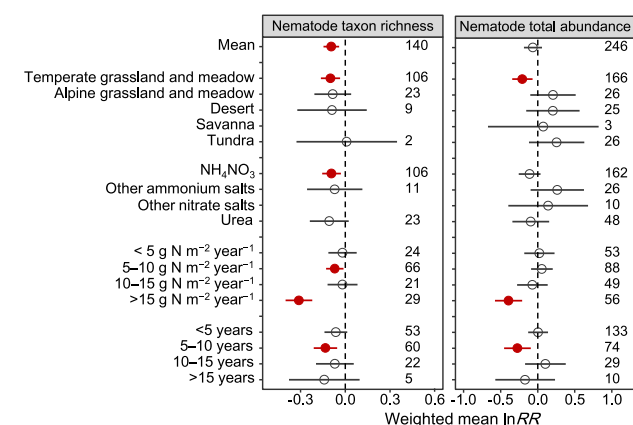


Fig. 1. Effects of N addition on soil nematode taxon richness and total abundance between different grassland ecosystems, N forms, N addition rates ($\text{g N m}^{-2} \text{ year}^{-1}$), and experimental durations (years). Values are weighted mean natural log response ratios ($\ln\text{RR}$) with $\pm 95\%$ confidence intervals. Filled circles represent significant effects by N addition ($P < 0.05$). Numbers on the right denote the number of observations of response variables. Blue and red indicate positive and negative significant effects, respectively. NH_4NO_3 , ammonium nitrate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

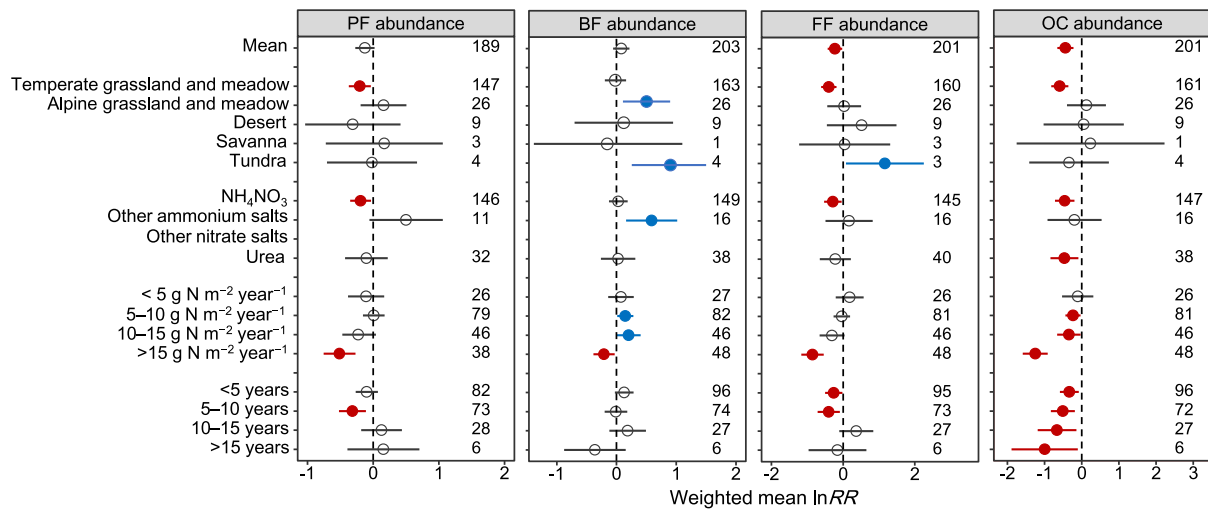


Fig. 2. Effects of N addition on abundances of PF, BF, FF, and OC nematodes between different grassland ecosystems, N forms, N addition rates ($\text{g N m}^{-2} \text{ year}^{-1}$), and experimental durations (years). Values are weighted mean natural log response ratios (lnRR) with $\pm$ 95% confidence intervals. Filled circles represent significant effects by N addition ($P < 0.05$). Numbers on the right denote the number of observations of response variables. Blue and red indicate positive and negative significant effects, respectively. PF: plant-feeding; BF: bacterial-feeding; FF: fungal-feeding; OC: omnivorous-carnivorous. NH₄NO₃, ammonium nitrate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

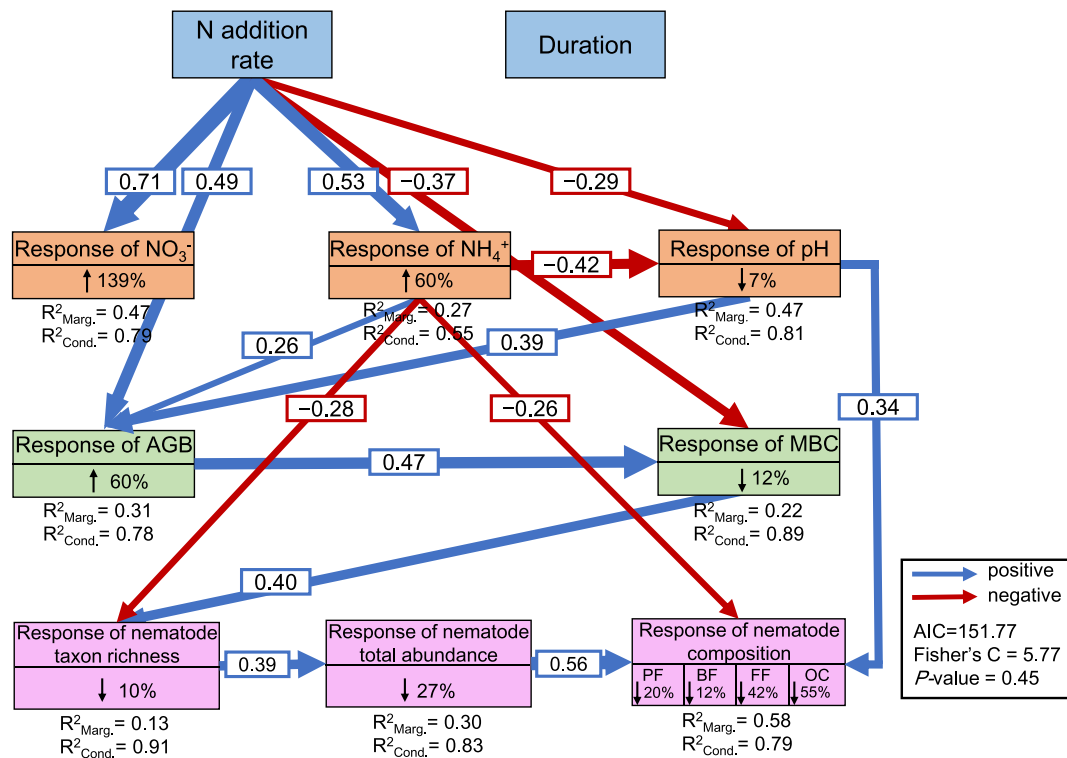


Fig. 3. Piecewise structural equation model (SEM) analysis of the effects of N addition rates (natural log transformed) and experimental durations (natural log transformed) on soil nematode variables via changes in the weighted natural log response ratios (lnRRs) of abiotic soil factors (soil NH₄⁺ concentration, NO₃⁻ concentration, and pH) and biotic factors (AGB and MBC). Numbers beside the arrows are standardized coefficients. The width of each arrow is proportional to the standardized path coefficient, with solid blue and red arrows representing positive and negative effects, respectively. Statistically significant level for the solid arrows is $P < 0.05$. Grey dashed arrows represent the insignificant effects ($P > 0.05$). Conditional R^2 ($R^2_{\text{Cond.}}$) and marginal R^2 ($R^2_{\text{Marg.}}$) represent the proportion of total variance explained by the dependent variable of interest when random effects are considered or not, respectively. The “↑” and “↓” symbols indicate increase or decrease, respectively, in response to N addition. The number in each square box indicates the percentage of change (%) to N addition. NH₄⁺, NO₃⁻, AGB, and MBC represent ammonium, nitrate, plant aboveground biomass, and microbial biomass carbon, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

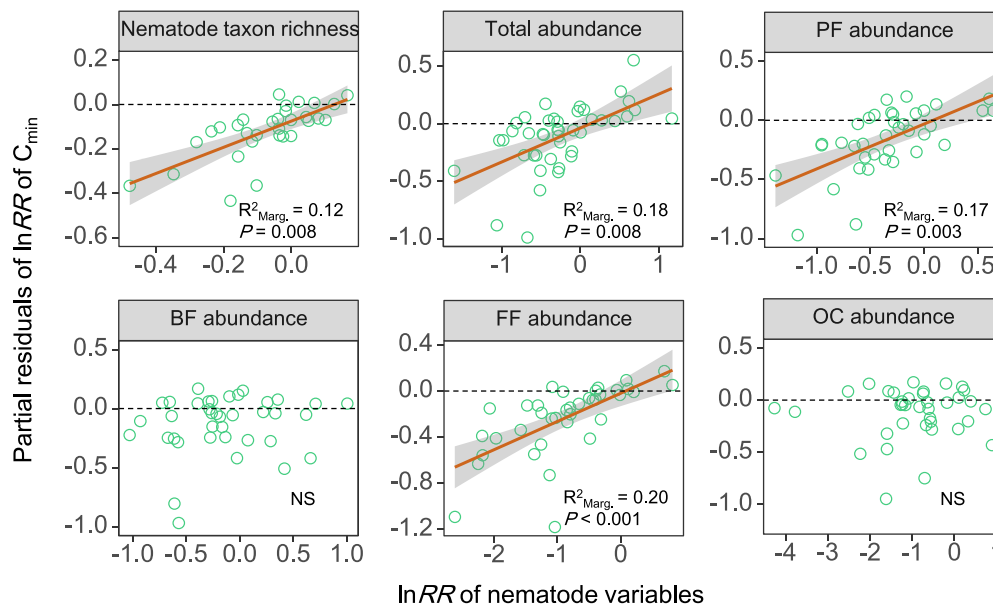


Fig. 4. Effects of responses of soil nematode taxon richness and abundance (community, PF, BF, FF, and OC groups) on response of soil C mineralization rate. Points represent values predicted by partial regressions for each explanatory variable after controlling the effects of responses of microbial biomass carbon. Fitted regressions and their 95% confident intervals (shaded) and corresponding levels of significance (P) are presented. The R^2 values represent the proportion of total variance explained by the dependent variable of interest when random effects are not considered ($R^2_{\text{Marg.}}$). C_{min} : carbon mineralization; PF: plant-feeding; BF: bacterial-feeding; FF: fungal-feeding; OC: omnivorous-carnivorous; MBC: microbial biomass carbon; NS, $P > 0.05$.

a pasture in New Zealand, which showed that N fertilization decreased the richness of FF and OC groups, and thus the total nematode richness (Sarathchandra et al., 2001). However, N addition of > 10 years had no effect on nematode richness. This result was in contrast with our hypothesis that the negative responses of nematode richness may be amplified with prolonged experiments. This contradiction may have been due to either the ecosystem entering an equilibrium after a given period of time or the experimental durations were short, which prevented the detection of general longer-term trends in nematode richness responses.

4.2. Effects of N addition on soil nematode abundance

We observed that N addition did not reduce the total nematode abundance, which was not in agreement with our first hypothesis. The potential reason for this pattern was that the responses of nematode trophic groups (PF, BF, FF, and OC) to N addition were inconsistent across different grassland ecosystems, under different N forms and N addition rates and different experimental durations.

For grassland ecosystems, N addition significantly reduced the abundances of PF, FF, and OC groups in temperate grassland and meadow, but increased the abundances of the BF group in alpine grassland and meadow and tundra. This might have been due to the following reasons. First, the average N fertilization rate in temperate grassland and meadow was higher than that in alpine grassland and meadow, and tundra (13.21 vs. 11.64 g N m⁻² year⁻¹, and 13.21 vs. 2.57 g N m⁻² year⁻¹, respectively). High N addition rates in temperate grassland and meadow could induce NH₄⁺ toxicities in nematodes, resulting in the reduction of PF, FF, and OC group abundances (Chen et al., 2019; Wei et al., 2012). Second, opportunistic nematodes such as the BF group often increased in abundance with low to medium levels of N addition in alpine grassland and meadow and tundra, as they exhibit resource-acquisitive strategies and rapid growth rates in response to increased microbial biomass (Ettema et al., 1999; Ruess et al., 2002). However, the responses of BF abundance to N addition may decrease with higher background soil N availability due to the reduced N

limitation for nematodes (Tian et al., 2016). In our study, we found that background soil N content in tundra and alpine grassland and meadow was higher than that in temperate grassland and meadow, savanna and desert ecosystems (Wang et al., 2019). It may lead to lower nematode responses to N addition in alpine grassland and meadow and tundra than other ecosystem types. Thus, despite the N addition stimulated abundance of BF nematodes in alpine grassland and meadow and tundra, it could be predicted that the beneficial effects of N addition on BF likely diminished or even become negative with high continuous N deposition in the future, when the soil N availability exceeded the N demands of BF nematodes.

For N forms, we found that the addition of NH₄NO₃ significantly decreased the abundances of the PF, FF, and OC groups, while the addition of other ammonium salts increased the abundances of the BF groups. The addition of NH₄NO₃ increased the soil NH₄⁺ concentration, which had an inhibitory effect on the growth of PF nematodes when they parasitized the roots and ingested NH₄⁺ rich cell fluids (Kronzucker et al., 2001; Wei et al., 2012). The addition of NH₄NO₃ simultaneously increased the soil NH₄⁺ concentration and induced soil acidification, which inhibited the growth of FF and OC nematodes due to their lower tolerance for ammonia and acid (Tenuta and Ferris, 2004). The direct adverse impacts of soil acidification on soil nematode communities generally result from the limitations of base cations (e.g., Na⁺, Mg²⁺, and Ca²⁺) and the toxic effects of non-base cations (e.g., H⁺, Al³⁺, and Mn²⁺) (Chen et al., 2015a). However, the positive effects of the addition of other ammonium salts on the abundance of BF from the limited studies collected might have been due to NH₄⁺ fertilized soil that promoted plant and microbial biomass, which were beneficial for the growth of BF.

For the N addition rate, we found that the abundance of BF increased, ranging from 5 to 15 g N m⁻² year⁻¹, while the abundance of OC decreased. BF has the advantage of consuming increased microbial biomass under low to medium N addition levels. In contrast, OC nematodes likely decreased under low N addition levels, since they had less developed secretory-excretory systems to cope with poisonous NH₄⁺ (Bongers and Ferris, 1999; Tenuta and Ferris, 2004). Further, the

abundances of PF, BF, FF, and OC decreased when the N addition rate was $> 15 \text{ g N m}^{-2} \text{ year}^{-1}$, which suggested that high N levels inhibited the abundances of all nematode groups (Chen et al., 2019; Wei et al., 2012).

We found that the experimental duration threshold for significant decreases in the abundances of FF and OC was less than five years, while the threshold for PF was < 10 years. The negative responses of OC, FF, and PF nematode abundance to N addition could be amplified with prolonged experiments due to cumulative N inputs that exceeded nematode N demands and/or the deterioration of nematode living conditions. However, our results clearly indicated that high trophic levels of FF and OC nematodes were more sensitive to N enrichment than low trophic levels of PF nematodes across global grasslands.

4.3. Potential mechanisms underlying the effects of N addition on soil nematode variables

Changes in soil NH_4^+ concentrations can mediate the effects of N addition on nematode communities. In support of our second hypothesis, the SEM indicated that the increased $\ln\text{RR}$ of the NH_4^+ concentration induced by the N addition rate had a negative effect on the $\ln\text{RR}$ of nematode taxon richness. In addition, the $\ln\text{RR}$ of the NH_4^+ concentration had a negative effect on PC1 scores, which suggested that increased soil NH_4^+ concentrations under N addition simultaneously decreased the $\ln\text{RR}$ s of PF, BF, FF, and OC abundances. Higher levels of NH_4^+ concentration in soil may be relatively transient, because NH_4^+ can be rapidly converted to NO_3^- . However, previous study found that higher osmotic potential caused by higher ammonium concentration significantly inhibited the activity and population of nematodes in one day (Tenuta and Ferris, 2004). Therefore, the negative correlation between higher ammonium concentration and nematode community composition suggests that the NH_4^+ concentrations in soil may have reached toxic levels for PF, BF, FF, and OC nematodes. As a result, increased soil NH_4^+ concentrations might significantly reduce the taxon richness and abundances of different trophic groups and shift the composition of nematode communities. The SEM also revealed that the increased availability of soil NH_4^+ promoted the $\ln\text{RR}$ s of AGB and MBC, which in turn increased the $\ln\text{RR}$ s of nematode taxon richness, $\ln\text{RR}$ of nematode abundance, and PC1. This might have been due to the increased soil NH_4^+ stimulated carbon fixed by plants, as plant carbon is a primary food resource to maintain the richness and abundance of many soil microorganisms and faunas (Scherber et al., 2010; Wardle et al., 2004). However, the positive effects of AGB and MBC on nematodes were invalidated by the negative effects of NH_4^+ in this study, which resulted in the overall negative effects of N addition on nematodes taxon richness and abundance.

Changes in soil pH concentrations can also regulate the effects of N addition on nematode communities. The SEM revealed that the addition of N affected soil nematode communities through the soil acidification pathway, which aligned with our second hypothesis. This trend was consistent with previous studies in grasslands (Grayston et al., 2001), forests (Sun et al., 2013), and agricultural ecosystems (Liu et al., 2016). Specifically, the N addition rate had a direct negative effect on the $\ln\text{RR}$ of the soil pH, while the $\ln\text{RR}$ of the soil pH had a direct positive effect on the PC1 scores. These results suggested that the N addition rate could reduce the $\ln\text{RR}$ s of PF, BF, FF, and OC abundances by decreasing the soil pH. On a global scale, the soil pH decreases linearly with N addition rate in most grassland ecosystems (Tian and Niu, 2015). Furthermore, we found that increased soil acidification under the addition of N indirectly inhibited the $\ln\text{RR}$ s of nematode taxon richness and abundances, and PC1 scores by decreasing the responses of AGB and MBC. Soil acidification typically reduces the availability of soil base mineral cations for plants, which leads to a decline in plant biomass (Bowman et al., 2008). Reduced plant biomass may further reduce the total microbial biomass (e.g., fungal and bacterial biomass) by decreasing C investments for microbes (Keith et al., 2009). As microbial biomass

provides energy sources and nutrients to many nematode trophic groups (e.g., BF, FF, and OC nematodes), a decline in MBC may translate to cascading negative effects on nematode taxon richness and abundances of multiple nematode trophic groups.

4.4. Links between the responses of soil nematode richness and abundance and the soil C mineralization rate

Nematode trophic groups with different feeding modes are important for the regulation of microbial biomass, which in turn affects microbial-mediated soil C mineralization ($C_{\min}$) processes. After controlling the effects of $\ln\text{RR}$ of MBC, partial regression analysis showed that variations in the $\ln\text{RR}$ of the soil $C_{\min}$ rate was primarily explained by the $\ln\text{RR}$ of nematode taxon richness, the $\ln\text{RR}$ of total abundance, and $\ln\text{RR}$ s of PF and FF abundances. The high diversity of nematode communities has been shown to stimulate a wider variety of microbes and thus increase microbial biomass (Bardgett et al., 1999; Ingham et al., 1985). Therefore, the decline of nematode taxon richness and abundance under N enrichment may weaken its positive impacts on microbial biomass and contribute to the reduction of $C_{\min}$ (Wang et al., 2017). We also found that the $\ln\text{RR}$ of PF abundance had a positive association with the $\ln\text{RR}$ of $C_{\min}$, which was likely due to the nutrient leakage from plant roots infected by PF nematodes, which can increase the food resource supplies for microbial metabolism, thereby increasing the C mineralization rate in the rhizosphere soil (Gan and Wickings, 2020; Yeates et al., 1999; Yeates et al., 1998). Although the grazing activities of BF nematodes can stimulate bacterial activities and promote $C_{\min}$ in grassland ecosystems (Bardgett et al., 1999), the absence of a relationship between the $\ln\text{RR}$ of BF nematodes and $C_{\min}$ in our study may have been due to the top-down effects of BF nematodes on bacteria being weaker under high soil ammonia and acidic conditions. Moreover, we found that the reduction in the $\ln\text{RR}$ of FF abundance induced by N addition was related to the decrease in the $\ln\text{RR}$ of $C_{\min}$. Fungi could promote the generation of hyphae when they were grazed by soil fauna, which in turn promoted fungal carbon consumption and $C_{\min}$ (Hedlund and Öhrn, 2000). High levels of N addition may reduce the abundance of FF nematodes and release the stimulatory effects of FF nematodes on fungal biomass, leading to the decline of $C_{\min}$. Unexpectedly, we found that the $\ln\text{RR}$ of OC abundance was unrelated to the $\ln\text{RR}$ of $C_{\min}$ under N addition. Although omnivores and carnivores can affect bacteria and fungi by feeding on diverse nematode groups through soil food webs (Leibold, 1989; Mikola and Setälä, 1998), the decoupled relationships between OC abundance and thereby microbial-mediated soil $C_{\min}$ might be due to the OC nematodes being highly sensitive to the addition of N.

5. Conclusion

Our results revealed that N enrichment had profound adverse effects on the taxon richness, and the abundance of fungal-feeding and omnivorous-carnivorous nematodes across global grasslands, and these inhibitive effects were more pronounced with the intensity of N input levels. Increases in soil ammonium concentrations and soil acidification were the main two mechanisms underlying the negative impacts of N enrichment on nematode communities. Decreases in nematode richness and abundance were intimately linked to the decline of their associated soil carbon mineralization. The patterns and causal mechanisms of this study call our attention to the detrimental impacts of increasing anthropogenically derived N inputs on soil nematode diversity and subsequent ecosystem functions across global grassland ecosystems. Therefore, we suggest that N-induced the increases in soil ammonium concentrations and soil acidification should be included in models that predict the linkages between belowground communities and carbon cycling in grassland ecosystems under future scenarios of N deposition.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2023.116564>.

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