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RESEARCH ARTICLE

Mowing did not mitigate the negative effects of nitrogen deposition on soil nematode community in a temperate steppe

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ABSTRACT

Soil nematodes are the most numerous components of the soil fauna in terrestrial ecosystems. The occurrence and abundance of nematode trophic groups determine the structure and function of soil food webs. However, little is known about how nitrogen deposition and land-use practice (e.g. mowing) affect soil nematode communities. We investigated the main and interactive effects of nitrogen addition and mowing on soil nematode diversity and biomass carbon in nematode trophic groups in a temperate steppe in northern China. Nitrogen addition and mowing significantly decreased the abundance of soil nematodes and trophic diversity but had no effects on nematode richness and the Shannon–Wiener diversity. Nitrogen addition influenced soil nematode communities through decreasing soil pH. Mowing influenced soil nematode communities through decreasing soil moisture. Nitrogen addition enhanced the bacterial energy channel but mowing promoted fungal energy channel in the soil micro-food web. Our study emphasizes that ecosystem function supported by soil organisms can be greatly influenced by nitrogen deposition, and mowing cannot mitigate the negative effects of nitrogen deposition on soil food webs.

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1 Introduction

Nitrogen deposition is an important threat to terrestrial ecosystems and projected to increase further in the coming years (Galloway et al., 2008). Nitrogen enrichment caused by nitrogen deposition is one of the main reasons leading to species extinction and changes in species composition in grassland ecosystems (Zhang et al., 2014). Shifts in plant composition has an important mediation effect on soil bacteria, fungi and their consumers (Bezemer et al., 2010; Zhang et al., 2015; Du et al., 2020). Nematodes, as the most important microbial predators in soil, are good indicators for evaluating the structure and function of soil food webs because they are closely related to the soil environment and are sensitive to habitat disturbance (Yeates, 2003; Bardgett and van der Putten, 2014). The predator–prey relationships between predatory nematodes, microbial-feeding nematodes, bacteria and fungi, linked the carbon and nutrient flow from

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microbial to higher trophic levels, which were important for soil ecosystem function (Heijboer et al., 2018; Richter et al., 2019). Since bacteria and fungi and their respective consumers have different turnover rates, the bacterial energy channel (bacteria to bacterivores to omnivores-predators) in soil food web is considered as a ‘fast cycle’ that processes labile organic matter, whereas the fungal energy channel (fungi to fungivores to omnivores-predators) is considered as a ‘slow cycle’ that processes more recalcitrant fractions of organic matter (Moore et al., 2003; Moore et al., 2005). The proportional relationship between those consumers, such as bacterivores and fungivores, can reflect the changes of soil decomposition pathways in soil micro-food webs (Wardle et al., 2004; Liang et al., 2009; Zhang et al., 2019a). Previous researchers have found that the increased availability of nitrogen can negatively affect nematode communities by increasing ammonium and aluminum toxicity and soil acidification, especially for plant-feeding nematodes (Sun et al., 2013; Chen et al., 2015). However, how nitrogen enrichment influenced the decomposition pathways in soil micro-food webs are still not clear.

Mowing is a management method for non-selective removal of plant biomass, which is a common practice in grassland. In the east of Inner Mongolia, mowing can produce hay as a sellable commodity for livestock feeding (Zhang et al., 2017). In some regions, mowing was also used to remove grazing selection effects on plant growth, and to manage grass growth (Landi et al., 2018). Mowing has been postulated to reduce the negative effects of nitrogen deposition on plant abundance and richness by removing biomass to reduce excess nutrients in the ecosystem (Härdtle et al., 2006; Lepš, 2014). Several studies have found that cutting grass for hay harvesting can protect plant diversity under nitrogen deposition (Poschlod et al. 2005; Knop et al. 2006). Although the influence of mowing on the aboveground subsystem has been studied widely, relatively little attention has been paid to the belowground subsystem. Due to the reduction of root exudation and accumulation of litter, mowing usually suppresses the abundance of soil biomass by reducing carbon supply for soil microorganisms and their grazers (Chen et al., 2019). However, our knowledge about how soil nematode community responses to mowing, especially to the interaction of nitrogen addition and mowing are still limited.

To evaluate how nitrogen addition and mowing influenced soil nematode community, we collected soil samples from a long-term experiment with nitrogen addition and mowing treatments in a semiarid grassland in northern China, and measured the abundance, diversity, and composition of soil nematode community. We hypothesized that i) the total abundance and diversity of nematode community will be negatively affected by the nitrogen addition and mowing, ii) nitrogen addition would promote soil bacterial energy channel in soil micro-food web by increasing labile organic matter to belowground, whereas mowing would promote fungal energy channel by stimulating fungi growth, iii) and mowing would mitigate the negative effects of nitrogen addition on nematode community by decreasing the nitrogen enrichment effects.

2 Materials and methods

2.1 Study site and experimental design

The field experiment was conducted in a natural steppe ecosystem near the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 116°14'E, 43°13'N) of the Chinese Academy of Sciences, Inner Mongolia, China. In the study area, the mean annual temperature and precipitation are 0.9°C and 355 mm, respectively, with 60%–80% falling from May and August. The plant community was dominated by *Leymus chinensis* (Trin.) Tzvel. and *Stipa grandis* P. Smirn (Poaceae), which accounted for more than 60% of total peak aboveground biomass. The soil is described as Haplic Calcisol according to the Food and Agriculture Organization of the United Nations (FAO) soil taxonomy classification. The experiment area had received no fertilizer or mowing before. Background nitrogen deposition was less than 1.5 g N m^{-2} yr^{-1} in this area (Lue and Tian, 2007).

The current study was conducted in a subsection of a long-term field experiment, which was established in September 2008 (Zhang et al., 2017). Briefly, the study area was fenced since 1999 to exclude livestock grazing. The experiment followed a randomized complete block design that consisted of four treatments, including control (no nitrogen addition and no mowing), + N (N addition and no mowing), + M (mowing and no nitrogen addition), and N + M (N addition and mowing). There were 6 replicate blocks for each treatment, for a total of 24 plots. Each plot was 8 m $\times$ 8 m in size and separated by a 1 m walkways. The nitrogen addition level was 10 g N m^{-2} yr^{-1}. The frequency of nitrogen addition was twice a year, simulating wet deposition in summer and dry deposition in winter, respectively. In June, NH_4NO_3 was mixed with 9.0 L of purified water and sprinkled uniformly to each plot using a sprayer to simulate wet nitrogen deposition. In November, NH_4NO_3 was mixed with 0.5 kg of clean sand and spread by hand to each plot to simulate dry deposition. The control and + M treatment received only purified water and clean sand. Mowing treatment was performed with a mower at 10 cm above the soil surface in late August to simulate typical hay-cutting management. All the aboveground biomass was removed after mowing.

2.2 Soil sampling

In August 2014, after the mowing treatment had completed, a composite soil sample at the depth of 0–10 cm layer (2.5 cm diameter corer) was taken from five randomly locations in each plot. All soil samples were transported to the laboratory in an incubator. In the laboratory, soil samples were passed through a 2 mm sieve to remove stones and roots and then stored in a refrigerator at 4°C for further analysis.

2.3 Soil chemical analysis

Total carbon (TC) and total nitrogen (TN) in soil were measured using a CN Elemental Analyzer (Leco Corporation, USA). The microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were extracted using a chloroform fumigation extraction method and then determined by CN Elemental Analyzer (Leco Corporation, USA). Soil pH was measured in a soil-water suspension (1:2.5 soil-water ratio) with a pH meter (Thermo Fisher Scientific Inc., USA). Soil moisture (SM) was determined by oven-drying at 105°C for 24 h.

2.4 Soil nematode extraction and identification

Nematodes were extracted from 100 g of fresh soil using a cotton-wool filter method (Oostenbrink, 1960). All nematodes in each sample were counted, and at least 100 nematodes per sample were identified to the genus level, according to Bongers (1994) and Ahmad and Jairajpuri, (2010). The nematodes were assigned to four trophic groups, including plant-parasites, fungivores, bacterivores and omnivores-predators (Ferris et al., 2001; http://plpnemweb.ucdavis.edu/nemaplex).

2.5 Statistical analysis

Nematode abundance was expressed as the number of individuals per 100 g dry soil. Nematode richness was expressed as the number of genera present in each sample. Shannon–Wiener diversity and trophic diversity were calculated from the nematode genus data set. Nematode biomass carbon of each trophic group was calculated from nematode abundance data based on nematode fresh weight database (http://nemaplex.ucdavis.edu/Ecology/) and Ferris (2010). Soil properties, nematode ecological indices and biomass carbon were analyzed using a two-way ANOVA to determine the effects of nitrogen addition, mowing and their interactions. A constrained redundancy analysis (RDA) was used to examine the effect of soil properties on nematode community composition. Nematode data were applied to Hellinger transformation before RDA analysis.

To test the effects of nitrogen addition and mowing on soil microbial biota, we constructed a structural equation model (SEM). We fitted the hypothesized model to the data and evaluated the model based on the χ^2 value, p-value and root-mean-square error of approximation (RMSEA). Since our initial model did not fit the data sufficiently well ($p < 0.05$), we removed the relationship with the lowest absolute test statistic based on regression weights and re-evaluated the new model.

For ANOVA, we tested the homogeneity of the variances using a Fligner-Killeen test and the normality of the residuals with a Shapiro–Wilk normality test. Post hoc comparisons were based on Tukey's HSD test. All statistical analyses were performed in R version 3.5.1 (R Core Team, 2019).

3 Results

3.1 Soil properties

Mowing treatment significantly influenced soil moisture with lower values observed in + M and N + M treatments than the control treatment (Table 1). Nitrogen addition significantly influenced the soil pH, MBC and MBN with lower values observed in + N and N + M treatments than in the control and + M treatments (Table 1). Mowing and nitrogen addition interacted to affect the ratio of soil C:N, and the decreased effects of mowing were much stronger under the treatments without nitrogen additions than that with nitrogen addition (Table 1). Neither mowing nor nitrogen addition significantly affected the soil TC and TN (Table 1). The ratio of MBC:MBN was lower in + N treatment than that in + M treatment (Table 1).

3.2 Nematode ecological indices and community composition

Both mowing and nitrogen addition significantly influenced the nematode abundance and trophic diversity with higher abundance and trophic diversity observed in the control treatment than + M, + N, and N + M treatments (Fig. 1). Mowing and nitrogen addition interacted to affect Shannon–Wiener diversity, but there were no significant differences between treatments in the post hoc test. RDA revealed that the mowing and the nitrogen addition treatments were clearly discriminated by the first and second principal components (Fig. 2A). Soil pH and soil moisture were important factors influencing the nematode composition (Fig. 2B). The eigenvalues of the first canonical axis and all canonical axes were

Table 1 Effects of nitrogen addition (N), mowing (M), and their interaction on soil moisture (SM), pH, total soil carbon (TC), total soil nitrogen (TN), C:N ratio (C:N), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and microbial biomass C:N ratio (MBC:MBN), as analyzed by two-way ANOVA.

	Treatment				Two-way ANOVA		
	C	N	M	NM	N	M	N × M
SM (%)	20.35±0.54a	19.13±0.60ab	18.20±0.64b	17.88±0.60b	0.21	**< 0.01**	0.46
pH	7.56±0.05a	6.27±0.15b	7.53±0.10a	6.29±0.13b	**< 0.001**	0.95	0.81
TC (g kg^{-1})	23.73±0.80	23.09±0.71	23.29±1.33	26.00±1.16	0.33	0.25	0.12
TN (g kg^{-1})	2.38±0.09	2.33±0.09	2.39±0.14	2.57±0.10	0.58	0.25	0.29
C: N	9.97±0.09ab	9.94±0.09ab	9.74±0.10b	10.11±0.08a	0.07	0.73	**0.04**
MBC (mg kg^{-1})	401.4±29.6ab	263.6±25.0c	424.2±25.6a	308.3±22.2bc	**< 0.001**	0.21	0.68
MBN (mg kg^{-1})	63.75±6.30a	33.43±3.78b	69.82±6.54a	40.95±2.49b	**< 0.001**	0.20	0.89
MBC:MBN	6.40±0.23ab	8.09±0.71a	6.22±0.36b	7.55±0.40ab	**< 0.01**	0.45	0.70

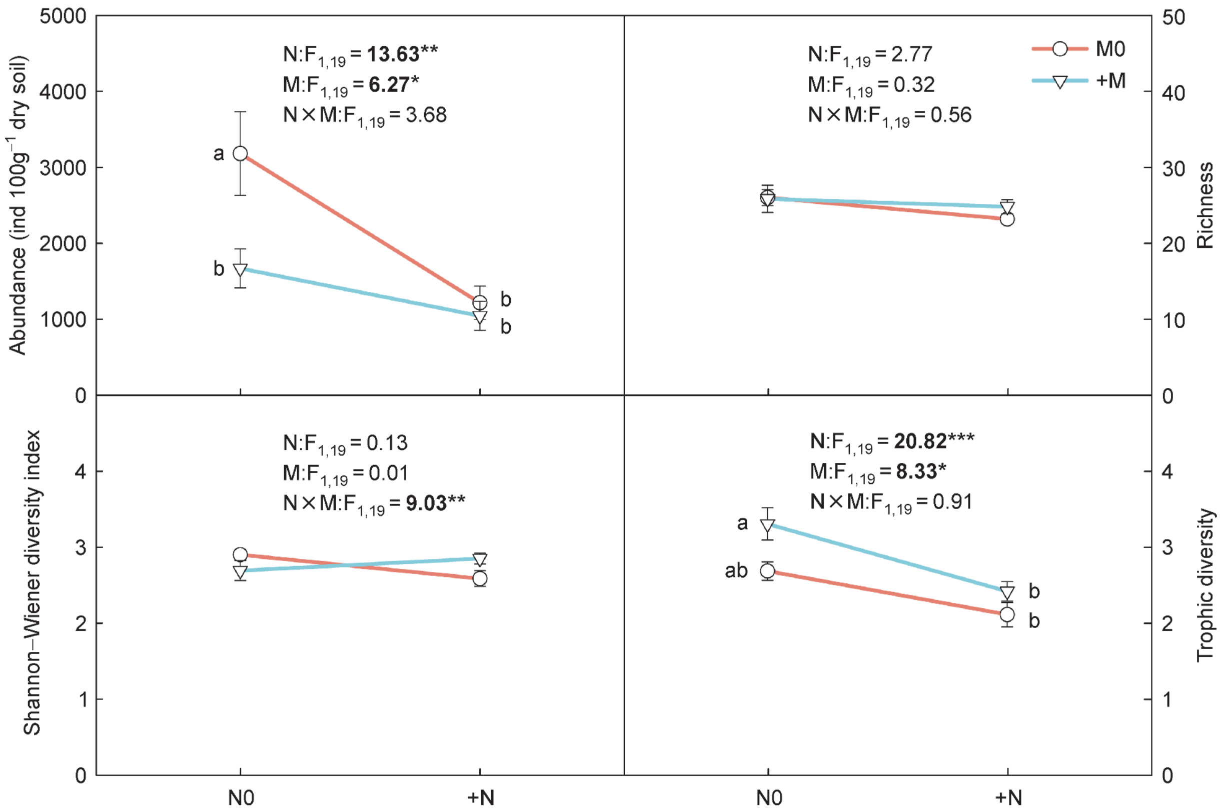

Fig. 1 Effect of nitrogen addition and mowing on nematode abundance, richness, Shannon–Wiener diversity, and trophic diversity. *F*- and *p*-values from a two-way ANOVA on the effects of nitrogen addition (N), mowing (M) and their interaction are also presented. Data are shown as mean + SE. Different letters indicate significant differences at $p < 0.05$ based on a Tukey's HSD test. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

0.143 ($F = 2.332$, $p = 0.036$) and 0.450 ($F = 1.431$, $p = 0.010$), respectively. The first axis explained 31.7% of the species-environment variation and the second axis explained 18.9% of the variation. The abundance of bacterivores, plant-parasites and omnivores-predators were highest in the control treatment, whereas the abundance of fungivores was higher in + M treatments in comparison with other treatments (Fig. S1).

3.3 Effects of nitrogen addition and mowing on nematode biomass carbon

Mowing treatment significantly decreased the biomass carbon of bacterivores and increased fungivores biomass carbon (Fig. 3). Mowing and nitrogen addition significantly decreased the biomass carbon of plant-parasites, and omnivores-predators (Fig. 3). We constructed the initial conceptual model with the hypothesized that nitrogen and mowing can affect biomass carbon of nematode trophic groups from pH and MBC to nematode biomass carbon. We did not find significant direct effects of nitrogen addition on the biomass carbon of bacterivores, fungivores, plant-parasites and omnivores-predators (Fig. 4, Table S2). Instead, nitrogen addition indirectly affects the biomass carbon in plant-parasites, bacterivores and omnivores-predators by reducing soil pH and MBC (Fig. 4, Table S2). Mowing negatively affected the biomass carbon of plant-parasites and bacterivores, whereas positively affected those of fungivores (Fig. 4, Table S2). It was noted that 58%, 55% and 34% of the variance in the biomass carbon of plant-parasites, fungivores and bacterivores were explained by SEM, respectively.

4 Discussions

4.1 Effects of nitrogen addition and mowing on soil nematode community

In agreement with our first hypothesis, our results showed that nitrogen addition negatively affected the nematode abundance. Previous studies have suggested that soil acidification and ammonium toxicity are the main factors that reduced the number of soil nematodes by nitrogen addition (Sun et al., 2013; Chen et al., 2015). Our results support this view by the fact that the decrease in soil pH after nitrogen addition significantly affects the soil nematode community (Table 1, Fig. 2). In addition, we found that the nitrogen addition effect has limited impacts on nematode richness and Shannon–Wiener diversity (Fig. 1).

Nitrogen addition can stimulate soil biota through enhan-

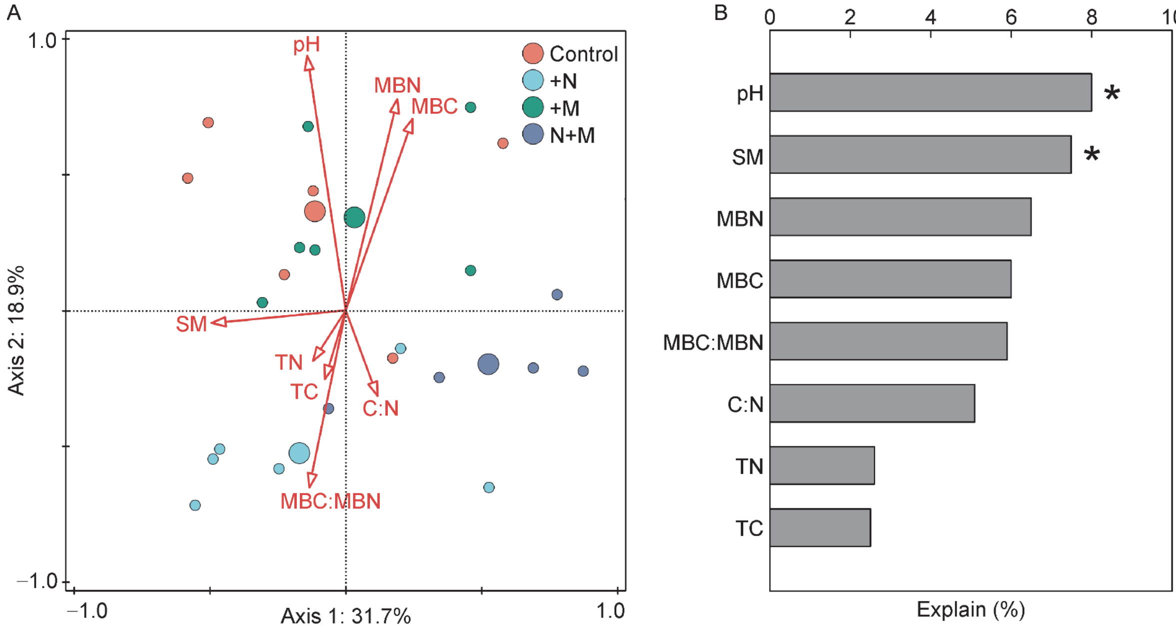

Fig. 2 Redundancy analysis of the relationship between nematode family and soil properties (A), and the explain percent of each soil indices on nematode community (B). The small cycle represents each sample and the large cycle represents the mean location of six replicated plots under the same treatment. Asterisk present significant effect on nematode community. SM, soil moisture; TC, total soil carbon; TN, total soil nitrogen; C:N, C:N ratio; microbial biomass carbon; MBN, microbial biomass nitrogen; MBC: MBN, microbial biomass C:N ratio. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

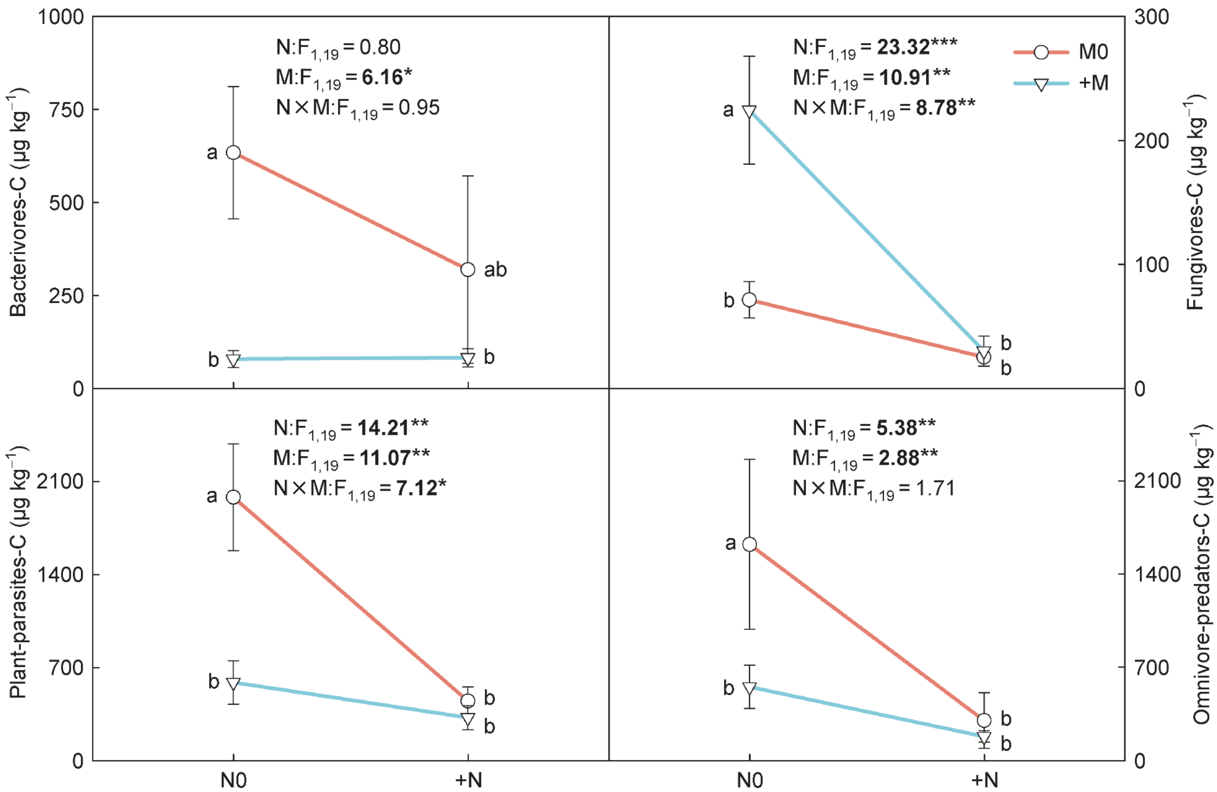

Fig. 3 Effect of nitrogen addition and mowing on biomass carbon in nematode trophic groups. *F*- and *p*-values from a two-way ANOVA on the effects of nitrogen addition (N), mowing (M) and their interaction are also presented. Data are shown as mean + SE. Different letters indicate significant differences at $p < 0.05$ based on a Tukey's HSD test. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

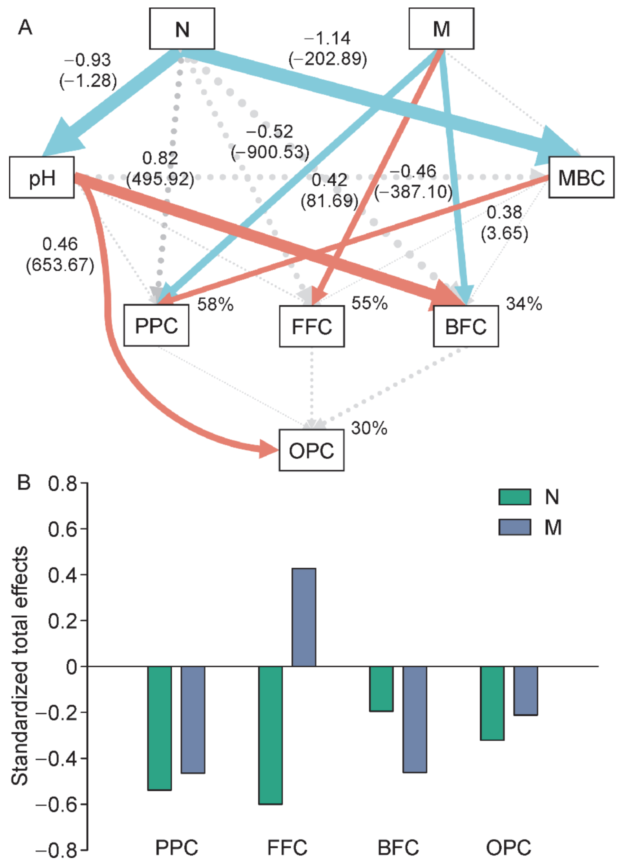

Fig. 4 Structural equation model linking nitrogen addition and mowing to biomass carbon in nematode trophic groups (A). Standardized total effects (direct plus indirect effects) derived from the structural equation models (B). Arrows indicate causal relationships among measured variables (orange arrows = effects; blue arrows = negative effects; continue arrows = significant relationships; dashed arrows = non-significant relationships, $p > 0.05$). Numbers next to arrows give the standardized and unstandardized regression coefficients outside and within parentheses, respectively. The width of the arrows indicates the strength of the causal influence. The model R^2 for each endogenous variable is given next to the variable. N, nitrogen addition; M, mowing; MBC, microbial biomass carbon; PPC, plant-parasites biomass carbon; FFC, fungivores biomass carbon; BFC, bacterivores biomass carbon; OPC, omnivores-predators biomass carbon. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

cing the input of nutrition and energy into the belowground (Hu et al., 2017). Therefore, some studies reported that neutral or even positive effects on nematodes diversity (Zhang et al., 2019b; Liu et al., 2020). Furthermore, plant community composition can significantly determine nematode community composition where soil nematode diversity generally has a positive relationship with above-ground plant diversity (Bezemer et al., 2010; Du et al., 2020). A recent study in the same long-term field experiment has shown that nitrogen addition decreased plant diversity (Zhang et al., 2014). Given the impacts of plant community on nematode community would be accumulated through time, our results show that at least six years of nitrogen addition will not have a significant impact on nematode diversity through changing the composition of aboveground vegetation.

Mowing significantly reduced nematode abundance, but did not affect nematode richness and Shannon–Weiner diversity. Plant litter input is one of the most important pathways for aboveground nutrients and energy to the belowground ecosystem and is the basis for soil biological growth (Bardgett and Wardle, 2010; Li et al., 2019). Mowing will reduce the return of above-ground biomass to the below-ground, and therefore reduce soil nematodes (Chen et al., 2019). Mowing also can increase soil surface temperatures by increasing ground irradiance (Wan et al., 2002), resulting in a decrease in soil moisture. Soil moisture is a basic condition for nematode movement, foraging and physiological stability (Xiong et al., 2020). Our results show that mowing affected the nematode community through changes in soil water conditions. The occurrence and abundance of nematode trophic groups can reflect the structure of soil food web and changes in ecosystem functions (Li et al., 2017b). Nitrogen addition and mowing significantly decreased the nematode trophic diversity, indicating that the composition of nematode trophic groups had changed significantly. Therefore, it is important to further analyze the response of different nematode trophic groups to nitrogen addition and mowing.

4.2 Effects of nitrogen addition and mowing on nematode biomass carbon in different trophic groups

The hypothesis that nitrogen addition would enhance the bacterial energy channel was not supported by our results, as we found no significant impacts of nitrogen addition on bacterivores biomass carbon. Since the bacterial energy channel dominate in enrichment and productive ecosystems such as grasslands (Pollierer et al., 2012). Many studies reported that nitrogen addition significantly increased the nitrogen concentration of plant litter (Li et al., 2017c; Hou et al., 2018). Therefore, the decomposability of litter was improved which is beneficial to bacterial energy channels. Although we have not observed an increase in biomass carbon of bacterivores, the structural equation modeling analysis revealed that there is a direct positive effect of nitrogen addition on biomass carbon of bacterivores, which indicated that the existence of beneficial effects (Fig. S3). However, this effect is masked by higher negative indirect effects of nitrogen addition through decreasing soil pH and microbial biomass. Combined with the direct and indirect effects of nitrogen addition on the biomass carbon of fungivores, plant-parasites and omnivores-predators, our results provide clear evidence of the negative effects of nitrogen addition on the belowground food web.

As our second hypothesis predicted, mowing significantly increased the biomass carbon of fungivores. Previous studies have demonstrated that mowing increased the mycorrhizal colonization and the transportation of carbon to AM fungi which stimulate the AM fungi hyphae to proliferate (Antonsen and Olsson, 2005; Binet et al., 2013). The increase of abundance and community diversity of fungi under mowing provide enough food sources for fungivores, which may reasonably explain the positive effects of mowing on the biomass carbon of fungivores (Li et al., 2017a). The fungal energy channel processes recalcitrant fractions of organic matter with a slow cycle (Moore et al., 2003; Moore et al., 2005). Therefore, although mowing reduced the carbon and nitrogen content in the soil by reducing input, it increased the ability of soil to stock carbon and nitrogen. Mowing had little effect on the bacterial community, suggesting that mowing may reduce the biomass carbon of bacterivores and plant-parasites by changing soil characteristics such as soil moisture.

Although we found significant interactive effects between mowing and nitrogen addition on soil nematode biomass carbon, nitrogen addition decreased the total abundance of soil nematodes and the biomass carbon in nematode trophic groups. The reduction was independent with or without mowing practice, which did not support our third hypothesis that mowing would mitigate the negative effects of nitrogen addition. Previous studies have demonstrated that hay-harvesting by mowing in grasslands would mitigate the negative impacts of nitrogen addition on plant species richness and evenness (Yang et al., 2019). Our results suggested that soil organisms had different responses to the interactive effects of nitrogen addition and mowing. Mowing did not mitigate the negative effects of nitrogen deposition on nematode trophic groups. It may be due to that mowing appears to be limited in mediating the impacts of nitrogen deposition on ecosystem nutrient cycling (Ilmarinen et al., 2009).

5 Conclusion

Nitrogen addition and mowing had significant impacts on soil nematode abundance and trophic diversity, but had no effects on nematode richness and Shannon–Wiener diversity. Nitrogen deposition and mowing affected the nematode community composition by affecting soil pH and soil moisture. Mowing cannot mitigate the negative effects of nitrogen deposition on soil food webs. Since nitrogen deposition is an important threat to terrestrial ecosystems, our study indicates that global changes can greatly influence ecosystem functions supported by soil organisms.

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Confict of interest

The authors declare no conflicts of interest.

Electronic supplementary material

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