RESEARCH ARTICLE

Trophic regulation of soil microbial biomass under nitrogen enrichment: A global meta-analysis

Wen Xing[1,2] | Xinli Chen[3] | Madhav P. Thakur[4] | Paul Kardol[5] | Xiaoming Lu[1] | Yongfei Bai[1]

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China

[2]Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, China

[3]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

[4]Institute of Ecology and Evolution and Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

[5]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence
Xiaoming Lu
Email: luxiaoming@ibcas.ac.cn

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Abstract

1. Eutrophication, including nitrogen (N) enrichment, can affect soil microbial communities through changes in trophic interactions. However, a knowledge gap still exists about how plant resources ('bottom-up effects') and microbial predators ('top-down effects') regulate the impacts of N enrichment on microbial biomass at the global scale.

2. To address this knowledge gap, we conducted a global meta-analysis using 2885 paired observations from 217 publications to evaluate the regulatory effects of plant biomass and soil nematodes on soil microbial biomass under N enrichment across terrestrial ecosystems.

3. We found that the effects of N enrichment on soil microbial biomass varied strongly across ecosystems. N enrichment decreased the soil microbial biomass of natural grasslands and forests due to soil acidification and the subsequent losses of predatory and microbivorous nematodes stimulating microbial growth. By contrast, N enrichment increased the microbial biomass of managed croplands mainly via increasing plant biomass production. Across diverse ecosystems, the short-term N enrichment (experimental duration ≤5 years) could reduce microbial biomass via decreasing nematode abundance, whereas the long-term N enrichment (experimental duration >5 years) mainly promoted microbial biomass via increasing plant biomass.

4. These findings highlight the critical roles of microbial predators and plant input in shaping microbial responses to N enrichment, which are highly dependent on ecosystem type and the period of N enrichment. Earth system models that predict soil microbial biomass and their linkages to soil functioning should consider the variations in plant biomass and soil nematodes under future scenarios of N deposition.

KEYWORDS
eutrophication, meta-analysis, nematodes, soil food web, soil microbial biomass, trophic regulation

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1 | INTRODUCTION

Over the last century, inputs of anthropogenic reactive nitrogen (N) into the biosphere have increased three- to five-fold, affecting multiple trophic levels of the soil food web in terrestrial ecosystems (Ackerman et al., 2019; Galloway et al., 2008). Soil microbes are the collection of diverse soil biologically communities including the bacteria, fungi, archaea, protists and viruses, among which bacteria and fungi typically dominate soil microbial biomass (Fierer, 2017; Jansson & Hofmockel, 2020; Sokol et al., 2022). Although the deposition of N can strongly affect microbial communities, it is not well-understood how variations in plant biomass ('bottom-up effects') and soil nematodes ('top-down effects') caused by N enrichment can explain the variation in microbial biomass in N-enriched terrestrial ecosystems. On the one hand, the deposition of N increases the availability of nutrients, promoting the biomass of soil bacteria and fungi by increasing plant biomass (Chen, Lan, et al., 2015; Zhou et al., 2017). On the other hand, N deposition can cause soil acidification and ammonium poisoning to bacteria and fungi, in turn, decreasing microbial biomass (Chen, Lan, et al., 2015; Rousk et al., 2010; Van Den Berg et al., 2005; Xing, Lu, Ying, et al., 2022). Moreover, increased ammonium poisoning and soil acidification following N enrichment can suppress the predation of free-living nematodes on both bacteria and fungi, reducing the turnover rates and thus biomass of microbial communities (Thakur & Geisen, 2019; Xing, Lu, Niu, et al., 2022). Therefore, it is critical to understand how microbial predators and plant input regulate microbial responses to N enrichment and their linkages to soil functioning under future scenarios of N deposition.

Soil microbes are under strong selections from both plant resource ('bottom-up') and nematode consumer ('top-down') controls (Allen et al., 2010; Chen, Lan, et al., 2015; Jiang et al., 2017; Lenoir et al., 2007; Rønn et al., 2012). Increased N inputs can stimulate the growth of resource-acquisitive species and promote plant biomass, particularly in N-limited ecosystems (Bai et al., 2010; Xia & Wan, 2008). This improves the quality and quantity of plant litter inputs to the soil, having potential bottom-up effects on microbial biomass (Chen et al., 2019; Liu & Greaver, 2010; Xing et al., 2019). Increased plant production can further promote below-ground carbon allocation (e.g. root exudates), stimulating the growth and activity of root-associated soil microbes (Bardgett & Wardle, 2010; Jiang et al., 2020; Keith et al., 2009; Magnani et al., 2007; Zak et al., 2008). However, excessive enrichment of N also leads to soil acidification, which reduces the biomass of plant species with high sensitivity to acidic soil; thus, constraining the allocation of organic carbon to soil microbial communities (Chen et al., 2016; Kuperman & Edwards, 1997). Several studies have demonstrated that N enrichment can alter plant community composition and lead to a reduction in bacterial and fungal biomass via soil acidification in grasslands (Chen et al., 2019; Song et al., 2023).

Free-living soil nematodes, including bacterial-feeding, fungal-feeding and omnivorous-carnivorous groups, are major consumers of soil microorganisms (Hu et al., 2022; Jiang et al., 2023; Thakur & Geisen, 2019; Xing, Lu, Niu, et al., 2022). For example, the predation of two bacterial-feeding nematode species (e.g. *Cruznema tripartitum* and *Acrobeloides bodenheimeri*) on bacteria can stimulate the activity and growth of bacterial community (Fu et al., 2005). Similarly, the grazing of fungal-feeding nematode (e.g. *Aphelenchus avenae*) on two fungi species (e.g. *Micheli corticolus* and *Moniliaceae* sp.) can increase the growth and abundance of such microorganisms (Li et al., 2004). Considering the increased quantities of reactive N strongly regulate the abundances of bacterial-feeding or fungal-feeding nematodes, it may be anticipated that such impacts will further affect soil microbial biomass. Additionally, omnivorous-carnivorous nematodes usually feed on microbial predatory nematodes, such as bacterial-feeding and fungal-feeding nematodes, exerting strong top-down controls of soil microbes (Thakur & Geisen, 2019). However, high levels of N enrichment can strongly suppress the abundance of omnivorous-carnivorous nematodes via the accumulation of soil H^+, Al^{3+} and ammonium (Xing, Lu, Niu, et al., 2022), which prohibit their growth and proliferation (Chen, Lan, et al., 2015; Xing, Lu, Niu, et al., 2022). As a result, the decrease in abundance of omnivorous-carnivorous nematodes could release their top-down controls on bacterial-feeding and fungal-feeding nematodes, subsequent weakening the trophic cascade effects on bacterial and fungal communities, leading to lower microbial biomass (Allen et al., 2010; Hu et al., 2022; Jiang et al., 2017; Lenoir et al., 2007). Although the critical role of plant inputs in regulating the impact of N enrichment on soil microbial biomass has been well studied, the contribution of microbe predators, such as free-living nematodes, has received less attention, especially on a global scale (Thakur & Geisen, 2019).

The relative importance of 'bottom-up' and 'top-down' controls could vary across ecosystems, depending on the responses of soil nematode communities to N enrichment and management practices. In natural grasslands and forests, nematode communities often include high abundance and richness of functional groups, which often feed on different microbial groups and may further alleviate competitive interactions between bacteria and fungi, accelerating the growth and turnover of microbial biomass (Crowther et al., 2015; Gralka et al., 2020; Kane et al., 2023). Increased soil ammonium concentrations and soil acidification resulting from N enrichment can dramatically inhibit the abundances of omnivores and predators (Chen et al., 2019; Tenuta & Ferris, 2004; Zhao et al., 2014), disrupting their trophic controls on microbial-feeding nematodes, ultimately affecting bacterial and fungal biomass (Hu et al., 2022; Thakur & Geisen, 2019). However, in croplands, intensive management (e.g. rotation and tillage) creates a highly temporal heterogeneous physicochemical environment for soil nematodes at the finer spatial scales (Liu et al., 2010; Zhang et al., 2021). This could reduce the abundances of omnivorous and predatory nematodes that are often susceptible to environmental stress, and thereby weaken their indirect controls over microbial biomass (Neher, 1999, 2010). However, the increased plant inputs under N enrichment may stimulate the growth of resource-acquiring bacterial groups and promote soil microbial biomass in croplands (Dai et al., 2018; Geisseler et al., 2016, 2017). Therefore, compared to natural grasslands and forests, the role of omnivorous and predatory nematodes

may be less important than plant inputs in regulating soil microbial biomass in croplands under N enrichment (Geisseler et al., 2016; Li, Chang, et al., 2018).

To our knowledge, few studies have evaluated the relative effects of bottom-up control (via plant inputs) and top-down control (via microbial-feeding nematodes) on microbial biomass under N enrichment across terrestrial ecosystems. This limits our understanding of above- and below-ground trophic interactions and their linkages to soil functions under conditions of global N enrichment. To address this knowledge gap, we compiled a global dataset of 2885 experimental observations from 217 publications encompassing natural grasslands, forests and croplands (Figure 1a). Specifically, our study addresses three questions: first, what is the general pattern of microbial biomass in response to N enrichment at global scale? Second, how do plant biomass (bottom-up) and soil nematode (top-down) regulate the effects of N enrichment on microbial biomass across diverse ecosystems, while simultaneously accounting for increased N availabilities and soil acidification that can modulate these effects (Figure 1b). Third, what are the potential mechanisms underlying the controls of plant biomass and different nematode feeding groups on microbial groups (e.g. bacteria and fungi) under N enrichment? Together, this meta-analysis may provide new insights regarding global change effects (e.g. N enrichment) on trophic regulation of the soil microbiome in terrestrial ecosystems.

2 | MATERIALS AND METHODS

2.1 | Data collection

We systematically searched all peer-reviewed studies on the effects of N enrichment on plant biomass, microbial biomass and nematodes, using the Web of Science, Google Scholar and the China National Knowledge Infrastructure Database (to 1 January 2023). We used the following search string: (nitrogen addition OR nitrogen application OR nitrogen deposition OR nitrogen enrichment OR nitrogen fertilisation OR nitrogen input OR nitrogen amendment) AND (fungi OR bacteria OR microbial biomass OR microbial community) AND (plant OR crop OR plant biomass OR above-ground biomass OR below-ground biomass OR root biomass OR yield OR nematod* OR fungivor* OR bacterivor* OR omnivor* OR predat* OR carnivor* OR nematode community OR nematode feeding groups OR bacterial-feeding nematode OR fungal-feeding nematode OR omnivorous nematode OR carnivorous nematode). The references listed in relevant previously published reviews and meta-analyses were also searched.

To avoid bias, the following criteria were employed: (1) the study was purposely designed to investigate the effects of N enrichment on soil microbes and reported the plant and/or nematode variables; (2) experiments were conducted in the field; (3) the N enrichment

FIGURE 1 Distribution map of N enrichment experiments across different ecosystems (grassland, forest and cropland) (a) and a conceptual model of how plant resources ('bottom-up') and microbe predators ('top-down') regulate the effects of N enrichment on microbial biomass in terrestrial ecosystems (b). On the one hand, N enrichment can increase the availability of nutrients, promoting the biomass of soil bacteria and fungi by increasing plant biomass (pathways a, b, f, i and o). On the other hand, N enrichment can cause soil acidification and ammonium poisoning to bacteria and fungi, in turn, decreasing microbial biomass (pathways b, c, h and k). Moreover, increased ammonium poisoning and soil acidification following N enrichment can suppress the predation of free-living nematodes on both bacteria and fungi, reducing the turnover rates and thus total soil microbial biomass (pathways b, c, g, j and n). Solid black and red arrows represent potential positive and negative effects, respectively.
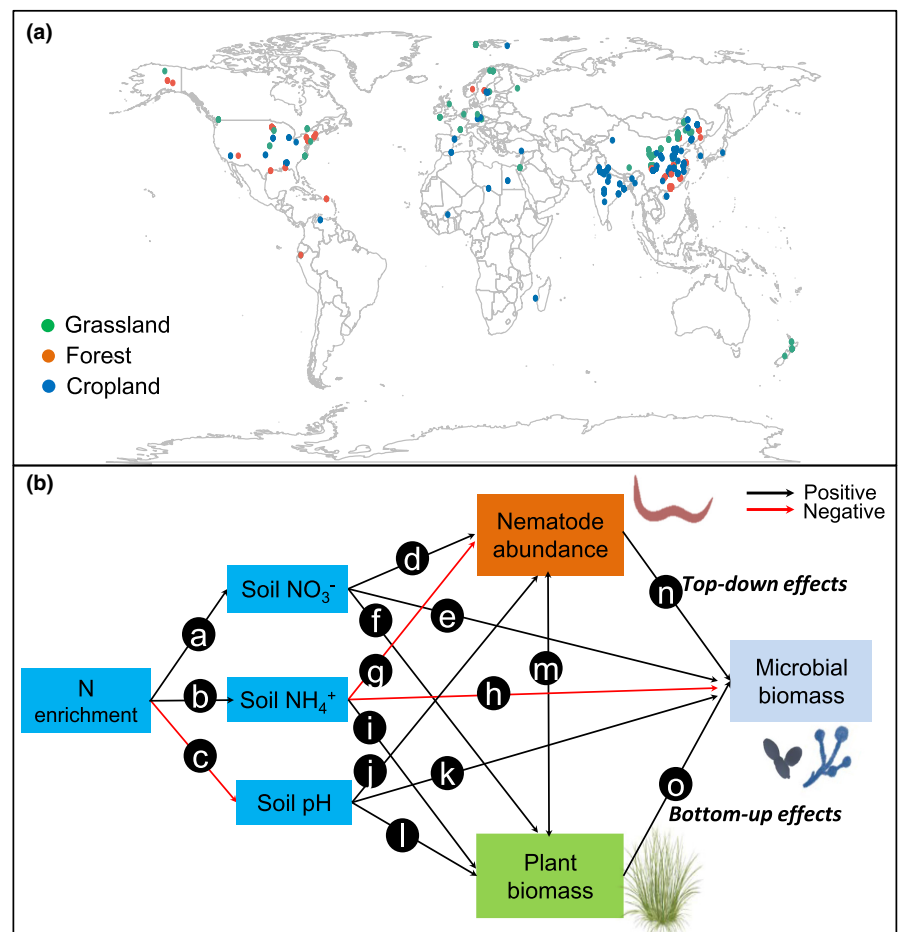
treatment and control plots shared the same microclimate, vegetation and soil type; (4) the means and sample sizes of response variables were provided. Literature selection was performed following the guidelines of PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) (Moher et al., 2009). Each site of the selected papers was treated as an independent study in our meta-analysis. If more than one independent experiment was conducted at different sites in one paper, they were treated as distinct studies. Those studies that were conducted at the same site under an identical experimental design but presented in separate papers were considered as one study. In total, 207 studies from 217 publications were included in our database. Data were directly extracted from the text and tables of publications or digitised by WebPlotDigitizer 4.1 (https://automeris.io/WebPlotDigitizer/) if presented in figures.

From each study, we extracted data on the experimental duration (years), soil microbial biomass carbon, nematode abundance, plant biomass and soil environmental factors. The microbial biomass variables included the total microbial, bacterial and fungal biomass. Strategies for determining the microbial biomass included the fumigation extraction technique and measuring the total amounts of phospholipid fatty acid (PLFA) in the soil. Nematode variables included the absolute abundance of bacterial-feeding, fungal-feeding, omnivorous-carnivorous and total nematodes. Plant biomass variables included above-ground biomass, root biomass or crop yields, while environmental factors included soil ammonium (NH_4^+) and nitrate (NO_3^-) concentration and soil pH. Ecosystem types encompassed grasslands, forests and croplands, respectively. Grasslands covered temperate grassland and meadow, alpine grassland and meadow, desert, savanna and tundra. Forests covered boreal forest, temperate forest and tropical forest.

2.2 | Replication statement

To understand how plant biomass and soil nematode regulate the effects of N enrichment on microbial biomass across diverse ecosystems, we collected the data of soil microbial biomass carbon, nematode abundance, plant biomass from 207 peer-reviewed N addition studies in 217 publications at global scale. N inputs were applied at the scale of field plot. The number of replicates of each level of N addition treatment was provided from the original collected papers (Table 1), ranging from 2 to 32 across different studies. In detail, the number of publications involving 3, 4, 5, 6 and other number of

replicates of each level of N addition treatment were 95, 60, 24, 34 and 4, accounting for 44%, 28%, 11%, 16% and 2% of the total publications, respectively.

2.3 | Data analysis

To assess the effect size of N enrichment on all response variables, we used the natural log-transformed response ratio (lnRR) (Hedges et al., 1999):

$$\ln RR = \ln(Xt / Xc), \qquad (1)$$

where Xt and Xc are the mean values of response variables in the N enrichment and control plots, respectively. However, individual observations are weighted differently, and this affects the estimates of effect sizes and subsequent inferences (Ma & Chen, 2016). Weighting functions based on sampling variance may assign extreme importance to a few individual observations, leading to the lnRR being primarily determined by a few studies. In our dataset, sampling variances were not reported in 51 out of the 217 studies. As an alternative, we used the sample sizes of response variables for weighting (Adams et al., 1997):

$$Wr = (Nc \times Nt) / (Nc + Nt), \qquad (2)$$

where Wr is the weight of each lnRR observation, while Nt and Nc represent the number of replications in the N enrichment treatments and control, respectively. To analyse the weighted mean lnRR and corresponding 95% confidence interval (CI) for each variable, we used a linear mixed effect model, employing the *lmer* function in the *lme4* R package (Bates et al., 2015). Since many of the included studies contributed more than one observation, the 'study' was treated as a random intercept to handle the potential autocorrelations between observations in each study.

To address the first question, we analysed the weighted mean N effect sizes for microbial biomass variables across all ecosystem types, including grasslands, forests and croplands. This was also done for nematode abundance and plant biomass, as well as abiotic soil factors (NH_4^+, NO_3^-, pH). The effect of N enrichment was considered significant if the 95% CI did not cover zero. To aid interpretation, we back-transformed the lnRR and corresponding CI to percentage changes, calculated as $(e^{\ln RR} - 1) \times 100\%$. We also analysed how N effects on microbial, nematode and plant variables varied with experimental duration (≤5 and >5 years) or soil environmental factors. In the linear mixed effect models, experimental duration and the lnRR of abiotic soil factors (NH_4^+, NO_3^-, pH) were treated as fixed effects,

TABLE 1 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Microbial biomass carbon	Plot	Ranging from 2 to 32 for each level of N addition treatment
Soil nematode	Plot	Ranging from 2 to 32 for each level of N addition treatment
Plant biomass	Plot	Ranging from 2 to 32 for each level of N addition treatment

with the 'study' as a random effect. Regression analysis was used to further assess the relationships between the lnRRs of microbial and plant biomass and nematode abundance in grassland, forest and cropland ecosystems, respectively.

To address the second question, we applied structural equation modelling (piecewise SEM) to test the relationships between the lnRRs of abiotic soil factors (NH_4^+, NO_3^-, pH), as well as the lnRRs of plant biomass, nematode abundance and microbial biomass between the natural and managed ecosystems and between the different experimental durations. Most variables examined in our study were correlated with one another in the grassland, forest and cropland ecosystems, making these datasets appropriate for SEM analysis (Figure S2). For different ecosystem types, we combined the data of the grassland and forest as a natural ecosystem and treated the data of the cropland as a managed ecosystem. For different experimental durations, we analysed the data for short-term (experimental duration ≤5 years) versus long-term (experimental duration >5 years) without considering the ecosystem types due to the datasets were limited for short-term vs. long-term in three ecosystem types, respectively. We developed an a priori conceptual model that depicted the causal relationships between these variables in a path diagram (Figure 1b), based on hypothesised mechanisms. The component models of the piecewise SEMs were fitted as linear mixed models, with the 'study' as a random effect (Lefcheck, 2016). We assessed model fit by Akaike information criterion (AIC), Fisher's C statistic and its associated p value for each model ($p > 0.05$ indicates adequate model fit). To avoid overfitting and increase the degrees of freedom, we simplified the initial model by removing any path with a coefficient >0.10 from the model when it was not significant

(García-Palacios et al., 2015; Shi et al., 2016). Data analyses were performed with R software (version 4.0.4; R Development Core Team, 2019), using the *nlme* and *piecewiseSEM* packages (Lefcheck, 2016).

Finally, to address the third question, we explored the effects of plant biomass and different nematode functional groups on microbial groups (i.e. bacteria and fungi) under N enrichment, by examining the relationships between the lnRRs of plant biomass and bacterial and fungal biomass; bacterial-feeding nematode abundance and bacterial biomass; and fungal-feeding nematode abundance and fungal biomass using regression analysis. We used Egger's regression to assess the potential for publication bias, using the *metafor* package (Koricheva et al., 2013). The results of Egger's regressions showed no significant publication bias in this meta-analysis (Table S1).

3 | RESULTS

3.1 | Effects of N enrichment on soil microbial biomass and properties

N enrichment did not impact the total microbial biomass, fungal biomass or bacterial biomass across ecosystem types (Figure 2a). However, the application of N significantly decreased the total and bacterial biomass in grasslands and forests (Figure 2b,c), while increased such variables in croplands (Figure 2d). Across ecosystem types, N enrichment did not affect the total, bacterial-feeding or fungal-feeding nematode abundances but did decrease the omnivorous-carnivorous nematode abundance (Figure 2a).
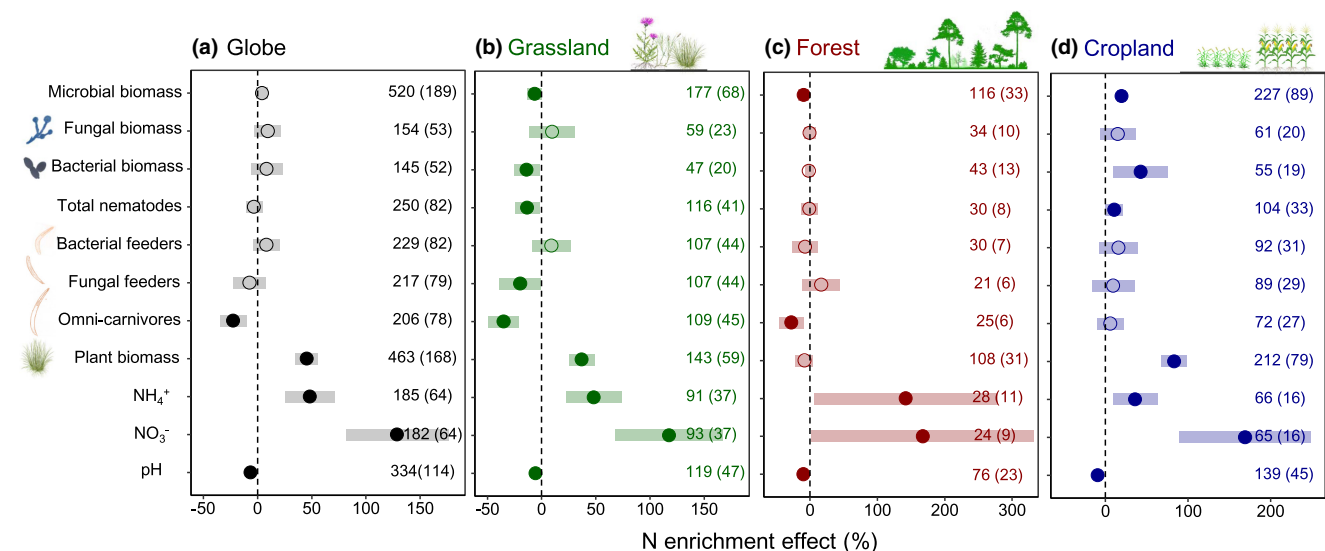

FIGURE 2 Effects of N enrichment on soil microbial biomass, nematode abundance, plant biomass and soil environmental factors across different ecosystems (a), and in grasslands (b), forests (c), and croplands (d). Values are weighted mean percentage changes (%) ± 95% confidence intervals. Filled circles represent significant effects by N enrichment ($p < 0.05$), and the number of studies is in parentheses. Numbers on the right denote the number of observations of response variables. NH_4^+, ammonium; NO_3^-, nitrate.

Specifically, the application of N decreased the total, fungal-feeding and omnivorous-carnivorous nematodes in grasslands (Figure 2b), as well as the omnivorous-carnivorous nematodes in forests (Figure 2c), but increased the total nematode abundance in croplands (Figure 2d). The enrichment of N significantly increased the plant biomass (Figure 2a), which was primarily due to its positive effects in grasslands and croplands (Figure 2b,d). The application of N significantly increased the concentrations of soil NH_4^+ and NO_3^-, but decreased the soil pH across various terrestrial ecosystems (Figure 2a–d).

With different experimental durations, the short-term of N enrichment (experimental duration ≤5 years) did not impact the total microbial biomass, fungal biomass or bacterial biomass (Figure S3a), while the long-term of N enrichment (experimental duration >5 years) significantly increased such microbial variables (Figure S3b). Both of the short- and long-term of N enrichments decreased the abundance of omnivorous-carnivorous nematode, but did not change the abundances of the bacterial-feeding and fungal-feeding nematodes. In addition, both the short- and long-term of N enrichment increased plant biomass and the concentrations of soil NH_4^+ and NO_3^-, but decreased the soil pH.

3.2 | Relationships between plant biomass, nematode abundance and microbial biomass

The lnRR of plant biomass was positively correlated with the lnRRs of microbial biomass carbon across all ecosystems (grasslands: $R^2 = 0.03$, $p = 0.06$; forests: $R^2 = 0.05$, $p = 0.02$; croplands: $R^2 = 0.08$, $p < 0.001$) (Figure 3a–c). The lnRR of total nematode abundance was positively correlated with the lnRRs of microbial biomass in grasslands ($R^2 = 0.11$, $p < 0.001$) and forests ($R^2 = 0.12$, $p = 0.06$) (Figure 3d,e), which was not the case with the lnRR of microbial biomass in croplands (Figure 3f).

3.3 | Plant biomass and soil nematode mediate effects of N enrichment on microbial biomass

In grasslands and forests, our structural equation modelling results indicated that the lnRR of soil pH had a direct positive effect on lnRR of microbial biomass (Figure 4a). However, the lnRR of soil NH_4^+ concentration had an indirect positive effect on lnRR of microbial biomass via its positive direct effect on plant biomass, and
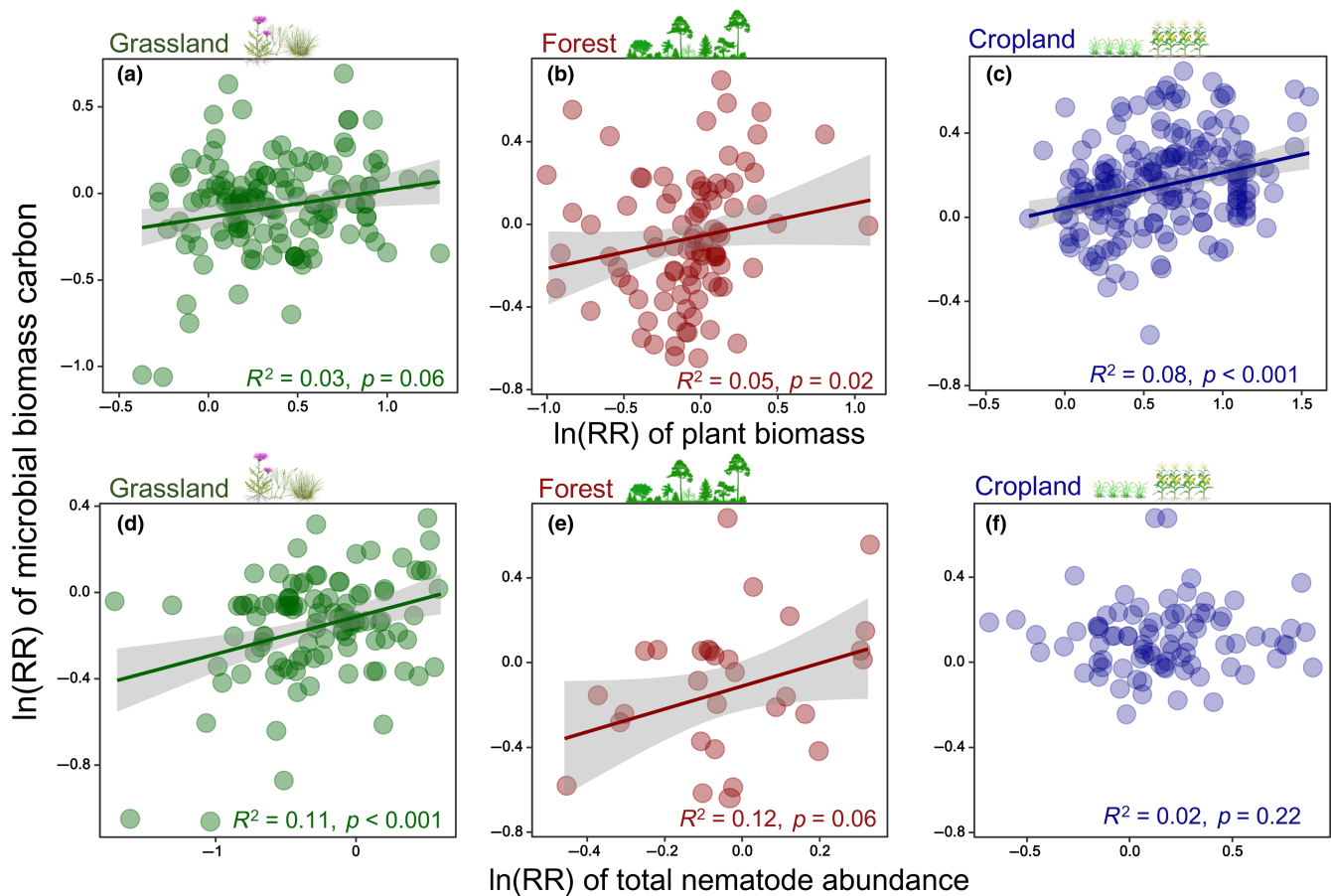

FIGURE 3 Relationships between the response ratios (lnRRs) of plant biomass, soil nematode abundance and soil microbial biomass in grasslands (a and d), forests (b and e), and croplands (c and f). Fitted regressions and their 95% confident intervals (shaded) and corresponding R^2 values and levels of significance (p) are presented.
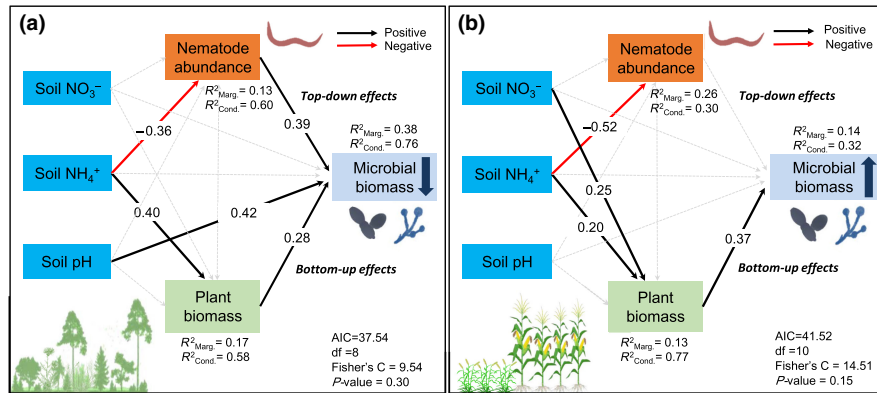
FIGURE 4 Structural equation model (SEM) analysis of plant biomass and nematode abundance mediate the effects of soil factors (soil NH_4^+ concentration, NO_3^- concentration and pH) on soil microbial biomass in natural grasslands and forests (a) and managed croplands (b). We used the response ratios (lnRRs) of each variable with N enrichment for model construction. Numbers beside the arrows are standardised coefficients. Solid black and red arrows represent positive and negative effects, respectively. Statistically significant level for the solid arrows is $p < 0.05$. Grey dashed arrows represent insignificant effects ($p > 0.05$). NH_4^+, ammonium; NO_3^-, nitrate.

indirect negative effect on lnRR of microbial biomass via its negative direct effect on nematode abundance. In croplands, the lnRRs of soil NH_4^+ and NO_3^- concentrations had indirect positive effects on lnRR of microbial biomass via their positive direct effects on lnRR of plant biomass (Figure 4b). Conversely, the lnRR of soil pH had no significant effect on microbial biomass via its effects on plant biomass and nematode abundance in either natural or managed ecosystems.

For the short-term of N enrichment, our structural equation modelling results indicated that the lnRR of soil pH had a direct positive effect on lnRR of microbial biomass (Figure S4a). However, the lnRR of soil NH_4^+ concentration had an indirect negative effect, and the lnRR of soil pH had an indirect positive effect on the lnRR of microbial biomass via their effects on nematode abundance. For the long-term of N enrichment, our structural equation modelling results indicated that the lnRR of the concentrations of soil NH_4^+ had indirect positive effects on lnRR of microbial biomass via their positive effects on the lnRR of plant biomass, despite the lnRR of soil NH_4^+ concentration had a direct negative effect on lnRR of microbial biomass (Figure S4b).

3.4 | Trophic regulation by plant biomass and nematode on microbial biomass

The lnRR of the plant biomass was positively correlated with the lnRR of bacterial biomass in grasslands (Figure 5a) and croplands (Figure 5c), but not in forests (Figure 5b). The lnRR of the plant biomass was positively related to the lnRR of fungal biomass in forests (Figure 5b) and croplands (Figure 5c), but not in grasslands (Figure 5a). The lnRRs of the bacterial and fungal biomass were positively related to the lnRR of the total microbial biomass across ecosystems (Figure 5a–c). The bottom-up regulation of plant biomass

likely promoted the microbial biomass by increasing the bacterial biomass in grasslands (Figure 5a); fungal biomass in forests (Figure 5b); and bacterial and fungal biomass in croplands (Figure 5c).

The lnRR of the omnivorous-carnivorous nematode abundance was positively related to the lnRRs of the bacterial-feeding and fungal-feeding nematode abundances in grasslands (Figure 5d) and forests (Figure 5e), as well as the lnRR of bacterial-feeding nematode abundance in croplands (Figure 5f). However, the lnRR of the bacterial-feeding nematode abundance was positively related only to the lnRR of bacterial biomass in grasslands (Figure 5d). The lnRR of the fungal-feeding nematode abundance was positively correlated with the lnRR of fungal biomass across the three ecosystems (Figure 5d–f). The top-down regulation of omnivorous-carnivorous nematodes on bacterial-feeding and fungal-feeding nematodes likely increased the bacterial and fungal biomass in grasslands (Figure 5d). The top-down regulation of omnivorous-carnivorous nematodes on fungal-feeding nematodes likely increased fungal biomass in forests (Figure 5e).

4 | DISCUSSION

Earlier studies have reported negative effects of N deposition on soil microbial biomass (Zhang et al., 2018), but they included a limited number of observations in croplands and forests (Treseder, 2008; Zhou et al., 2017). Thus, the general trends of microbial biomass responses to N enrichment could not be detected across terrestrial ecosystems. In contrast, our study included 2885 paired observations from 217 studies on grasslands, croplands and forests and found that the responses of soil microbial biomass to N applications were strongly dependent on plant biomass and nematode abundance, and varied considerably between the natural and managed ecosystems.
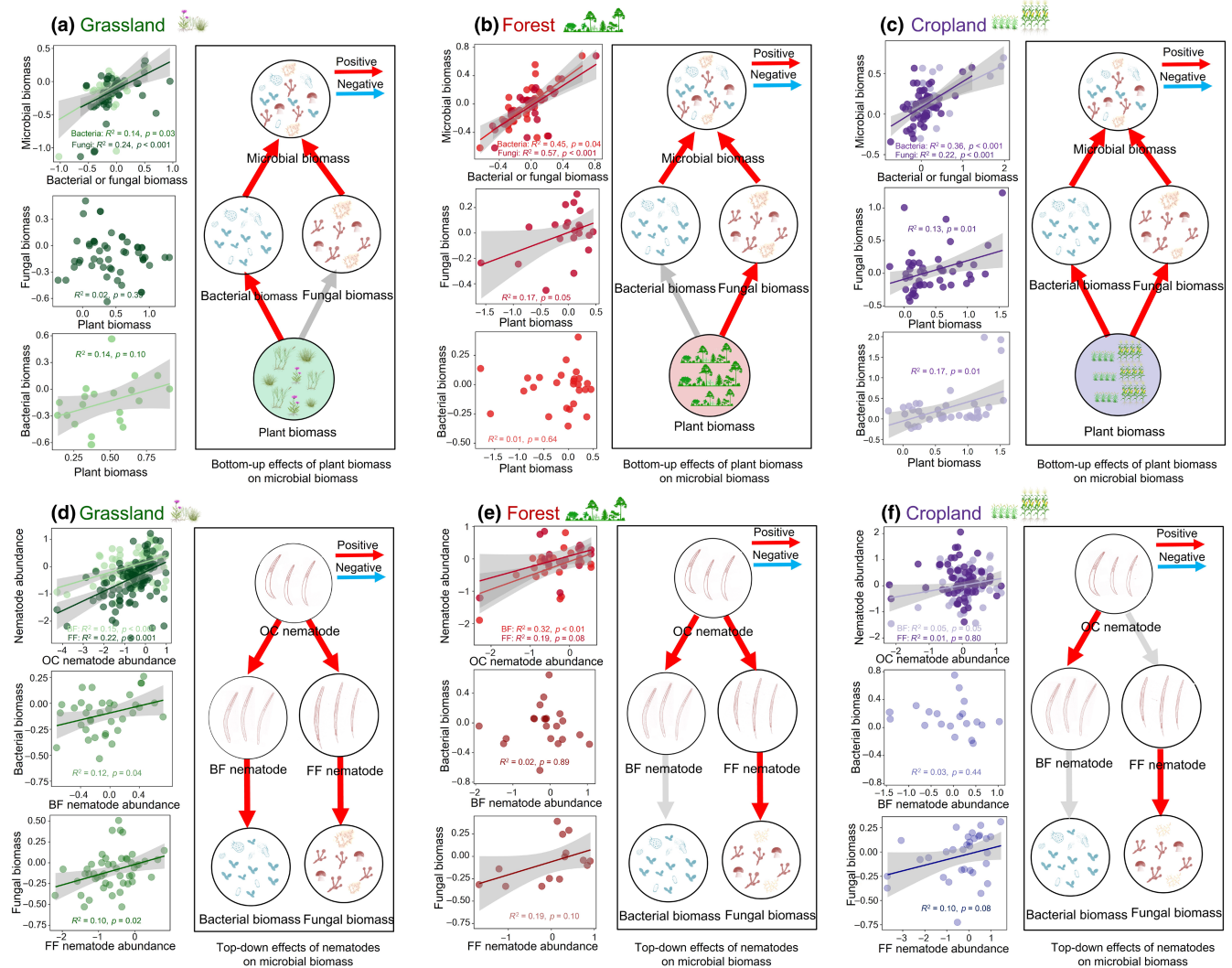
FIGURE 5 Relationships between the response ratios (ln*RR*s) of plant biomass and bacterial and fungal biomass, and the relationships between the response ratios (ln*RR*s) of bacterial and fungal biomass and total soil microbial biomass in grasslands (a), forests (b) and croplands (c). Relationships between the response ratios (ln*RR*s) of omnivorous-carnivorous nematode abundance and bacterial-feeding and fungal-feeding nematode abundances, and the response ratios (ln*RR*s) of fungal-feeding nematode abundance and fungal biomass, and the response ratios (ln*RR*s) of bacterial-feeding nematode abundance and bacterial biomass in grasslands (d), forests (e) and croplands (f). Conceptual diagrams illustrating the potential bottom-up regulation of plant biomass and the top-down regulation of omnivorous-carnivorous nematode on microbial biomass across different ecosystems. Fitted regressions and their 95% confidence intervals (shaded) and corresponding R^2 values and levels of significance (*p*) are presented. BF, bacterial-feeding nematode; FF, fungal-feeding nematode; OC, omnivorous-carnivorous nematode.

4.1 | Responses of soil microbial biomass in natural ecosystems

Previous studies have reported that the enrichment of N significantly decreased the microbial biomass of natural ecosystems (Chen et al., 2023; Compton et al., 2004; Gallardo & Schlesinger, 1994; Turner & Joseph Wright, 2014). However, these studies did not compare the relative importance of abiotic variables, plant inputs and nematode abundances on microbial biomass. Our findings revealed that the enrichment of N decreased the soil pH, which in turn suppressed the total microbial biomass in natural ecosystems (Figure 4). Soil acidification can reduce microbial biomass through the

increased proton (H^+) concentrations (toxic effect), the leaching of base cations (e.g. Na^+, Mg^{2+} and Ca^{2+}; nutrient deficiencies) and the mobilisation of metal cations (e.g. Fe^{3+}, Al^{3+} and Mn^{2+}; toxic effect) (Chen, Lan, et al., 2015; Chen, Wang, et al., 2015; Tian & Niu, 2015; Van Breemen & Van Dijk, 1988). Furthermore, our results showed that N enrichment strongly decreased the soil nematode abundance but increased the plant biomass in natural ecosystems, which is corroborated by recent studies (Chen, Lan, et al., 2015; Xing, Lu, Niu, et al., 2022). Compared to plant primary producers, nematodes are more sensitive to N inputs, as the increased soil acidification and ammonium concentrations have detrimental effects on their fitness and activities (Chen, Lan, et al., 2015; Nagy, 1999; Xing, Lu,

Niu, et al., 2022). More importantly, our results revealed that the decreased nematode abundance caused the reduction of soil microbial biomass, which could be due to the losses of predation of nematodes on microorganisms alleviated the 'top-down' controls of predators on microbial communities and thus prohibited the growths of microbes under N enrichment (Allen et al., 2010; Crowther et al., 2013; Lenoir et al., 2007; Saleem et al., 2013).

For different nematode trophic groups, our results suggested that the predation of omnivorous-carnivorous nematodes on microbial-feeding nematodes might have initiated cascading effects on bacterial and fungal communities, which in turn promoted turnover of microbial biomass in natural ecosystems (Chen, Lan, et al., 2015; Yeates, 2007; Yeates et al., 1993). Specifically, we found that the abundance of omnivorous-carnivorous nematode was positively correlated with the abundances of bacterial-feeding and fungal-feeding nematodes in grasslands, which were positively correlated with the bacterial and fungal biomass, respectively (Figure 5). We also found that the abundance of omnivorous-carnivorous nematode was positively correlated with the abundances of bacterial-feeding and fungal-feeding nematodes in forests, and the abundance of fungal-feeding nematode was positively correlated with the fungal biomass (Figure 5). Therefore, the loss of the top predatory nematodes via N enrichment could diminish their top-down controls on bacterial-feeding and fungal-feeding nematodes in natural grasslands and forests, which translated to a reduction in microbial biomass (Hu et al., 2022; Thakur & Geisen, 2019). However, we found that plant biomass had positive effects on the bacterial, fungal and total microbial biomass in grasslands and forests (Figure 5). Although N enrichment can increase plant litter, and thus the organic carbon to soil microbial communities in natural ecosystems, this positive effect is often offset by the adverse effects of soil acidification and the loss of nematode predation, resulting in net negative effects on microbial biomass (Chen et al., 2019; Chen, Lan, et al., 2015).

4.2 | Responses of soil microbial biomass in managed ecosystems

Compared to natural ecosystems, we found that N enrichment significantly increased microbial biomass in croplands, which was consistent with the results of several previous studies (Geisseler et al., 2017; Jia et al., 2020; Li, Jian, et al., 2018). The contrasting effects of N enrichment on microbial biomass in croplands compared to grasslands and forests may be due to two underlying drivers. First, the high sensitivities of microbial biomass to N enrichment in grasslands and forests soil may be because they are less resilient to stress, having been exposed to less stress conditions with atmospheric N deposition being the primary pathway for N inputs (Chen, Lan, et al., 2015; Rousk et al., 2010; Van Den Berg et al., 2005). However, the main forms of N inputs in managed cropping ecosystems are high levels of mineral N fertilisation, which can create extreme osmotic potentials that favour specific microbial groups with high tolerances

against acidity and ammonium towards maintaining microbial biomass (Hayatsu et al., 2017). Secondly, the plant biomass of croplands increases with higher N supplies (Liu et al., 2010; Zhang et al., 2021), which likely stimulates organic carbon inputs and promotes soil organic carbon and microbial biomass (Geisseler et al., 2016; Li, Chang, et al., 2018).

Notably, our findings suggested that nematode abundance did not mediate the effects of N enrichment on microbial biomass in croplands (Figure 4). These results were in contrast to the suggestion that the predation of free-living nematodes enhanced microbial biomass, but they suggested that nematode-induced trophic regulation of microbial biomass varied between ecosystem types (Jiang et al., 2023; Rossine et al., 2022; Thakur & Geisen, 2019). Croplands are highly disturbed due to the fragmentation of habitats and degradation of soil structures (Foley et al., 2005). As environmental conditions deteriorate in croplands, nematode communities could be simplified with an increase in the abundance of bacterivores and a decrease in the number of omnivores and predators (Neher, 1999, 2010). As a consequence, the top-down controls of omnivorous-carnivorous nematodes on microbial-feeding nematodes may be not strong under high levels of N enrichment (Thakur & Geisen, 2019). Indeed, our results showed that the abundance of omnivorous-carnivorous nematode was positively related only to the abundance of bacterial-feeding nematode rather than fungal-feeding nematode (Figure 5). However, the abundance of fungal-feeding nematode was positively related to fungal biomass. These results suggested that the top-down regulation of omnivorous-carnivorous nematodes on microbial-feeding nematodes, and consequently on bacterial and fungal biomass, were decoupled at triple trophic levels in croplands.

4.3 | Responses of soil microbial biomass to short- and long-term of N enrichment

We found that the short-term of N enrichment (experimental duration ≤5 years) did not change soil microbial biomass across the grassland, forest and cropland ecosystems. This could be due to the divergent responses of soil microbial biomass to N enrichment in different ecosystems. For example, a previous meta-analysis found that soil microbial biomass decreased significantly by 12% with N addition in global grasslands and increased by 13.6% in annual croplands (Geisseler et al., 2016). However, our results showed that the increased soil acidification and the concentrations of soil NH_4^+ mainly reduced soil microbial biomass via decreasing nematode abundance in natural ecosystems. This result was agreed with previous findings (Li et al., 2013; Sarathchandra et al., 2001; Song et al., 2016), which suggested that soil nematodes were sensitive to the short-term of soil nutrient inputs in natural grasslands and forests, leading to the decrease in their top-down controls on microbial biomass. By contrast, we found that the long-term of N enrichment (experimental duration >5 years) increased soil microbial biomass across the studied ecosystems, which could be due to the strong positive response of soil microbial biomass in

cropland. With respective to the multiple trophic levels, our results further showed that the increased concentrations of soil NH_4^+ remarkably increased plant biomass, which in turn promoted soil microbial biomass. This result was partially consistent with previous studies showed that plant productivity in cropland ecosystems was stimulated by the long-term of N fertilisation, which promoted plant residue inputs and thus stimulated soil microbial biomass (Geisseler et al., 2016). Notably, we did not find that soil nematode abundance mediated the effects of N enrichment on soil microbial biomass. Because nematode communities are sensitive to the long-term of N enrichment across different ecosystems (Xing et al., 2023; Zhou et al., 2021), the simplified nematode communities with lower abundance may have minor contributions to the variation of soil microbial biomass (Thakur & Geisen, 2019).

5 | CONCLUSIONS

In conclusion, our results demonstrate that the responses of soil microbial biomass to the application of N are strongly dependent on plant biomass and predatory nematodes, and vary considerably between ecosystems and experimental durations. N enrichment decrease the microbial biomass in natural ecosystems by decreasing the abundances of predatory and microbivorous nematodes that stimulate the growth and turnover of microbes through predation. This could weaken the linkages between above- and below-ground subsystems and is not conducive to maintain several ecosystem functions like primary productivity and carbon sequestration in grasslands and forests. While N fertiliser is critical for increasing microbial biomass in managed croplands, the decoupled trophic interactions under N enrichment are detrimental to the stabilities of soil productivity and soil health. Additionally, the short-term of N enrichment constrains soil microbial biomass via decreasing nematode abundance across diverse ecosystems, whereas the long-term of N enrichment stimulates soil microbial biomass through increasing plant inputs. Our findings highlight the need to find alternative sustainable ways, such as using organic fertilisers (e.g. animal manure and crop residues), to protect multitrophic interactions of soil micro-food web and build ecological resilience in natural and managed ecosystems.

AUTHOR CONTRIBUTIONS

Xiaoming Lu and Yongfei Bai conceived the ideas and designed the research. Wen Xing collected the data and conducted the data analysis. Wen Xing led the writing of the manuscript. Xiaoming Lu, Yongfei Bai, Xinli Chen, Madhav P. Thakur and Paul Kardol were involved in final writing and revision. All authors contributed critically to the drafts and gave final approval for publication.

ORCID

Wen Xing https://orcid.org/0000-0003-3448-6638
Xinli Chen https://orcid.org/0000-0003-0542-5959
Madhav P. Thakur https://orcid.org/0000-0001-9426-1313
Paul Kardol https://orcid.org/0000-0001-7065-3435
Xiaoming Lu https://orcid.org/0000-0001-7380-0699
Yongfei Bai https://orcid.org/0000-0001-6656-4501

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: PRISMA flow diagram for publication inclusion.

Figure S2: Correlations of relative changes in soil ammonium, soil nitrate, soil pH, and microbial (total biomass, fungal biomass, and bacterial biomass), nematode variables (total nematode abundance, and the abundances of bacterial-feeding, fungal-feeding, and omnivorous-carnivorous nematodes), and plant biomass under the enrichment of N in grasslands (a), forests (b), and croplands (c).

Figure S3: Effects of N enrichment on soil microbial biomass, nematode abundance, plant biomass and soil environmental factors between the short-term (experimental duration ≤5 years) (a) and the long-term (experimental duration >5 years) (b) of experimental duration across different ecosystems.

Figure S4: Structural equation model (SEM) analysis of plant biomass and nematode abundance mediate the effects of soil factors (soil NH_4^+ concentration, NO_3^- concentration, and pH) on soil microbial biomass between the short-term (experimental duration ≤5 years) (a) and the long-term (experimental duration >5 years) (b) of experimental duration across different ecosystems.

Table S1. Results of testing publication bias on our findings through Egger's regression.