Kong, Weibo; Eisenhauer, Nico; Peñuelas, Josep; [et al.]. «Climate and soil pH modulate global negative effects of nitrogen enrichment on soil nematodes». Soil biology and biochemistry, Vol. 208 (September 2025), art. 109860. DOI 10.1016/j.soilbio.2025.109860

Title: Climate and soil pH modulate global negative effects of nitrogen enrichment on soil nematodes

Running title: Effects of nitrogen enrichment on soil nematodes

Weibo Kong[1,2,3], Nico Eisenhauer[4,5], Josep Peñuelas[6,7], Liping Qiu[1,2,3], Xiaomei Gou[1,2,3], Yu Song[1,2], Jintao Jiao[1,2], Xiaoxu Jia[1,8], Xiang Wang[9], Mingan Shao[1,2,3,8], Gehong Wei[1], Xiaorong Wei[1,2,3]*

Affiliations:

1. State Key Laboratory of Soil and Water Conservation and Desertification Control, Northwest A&F University, Yangling, China.
2. College of Soil and Water Conservation Science and Engineering, Northwest A&F University, Yangling, China
3. Institute of Soil and Water Conservation, Ministry of Water Resources and Chinese Academy of Sciences, Yangling, China
4. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany;
5. Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany
6. CSIC, Global Ecology Unit, CREAF-CSIC-UAB, Bellaterra, Catalonia, Spain
7. CREAF, Cerdanyola del vallès, Barcelona, Catalonia, Spain

8. Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China
9. College of Land Science and Technology, China Agricultural University, Beijing, China

***Corresponding author:**

Xiaorong Wei (Orcid ID: 0000-0002-0359-0339)

26 Xinong Road, Yangling 712100, Shaanxi Province, China

Tel: 86 29 87012411; Fax: 86 29 87012210

E-mail: weixr@nwsuaf.edu.cn

Abstract

Soil nematodes account for ~80% of all Metazoans and play key roles in supporting terrestrial ecosystem functions, yet their responses to pervasive nitrogen (N) deposition, a significant global change factor, and their potential context-dependencies remain unclear. In this study, we conducted a global meta-analysis of 629 paired observations from 93 studies to examine how climatic and pedological factors modulate the effects of N enrichment on soil nematodes, and to assess the spatial patterns of these N-induced effects. We found that N enrichment significantly decreased soil nematode diversity (-3.2%), maturity index (-6.1%), structure index (-12.3%), and the abundance of omnivorous-predatory nematodes (-28.3%), but had minimal effect on the nematode enrichment index and the abundance of total and other trophic groups of nematodes. The negative effects of N on soil nematodes were greater in grasslands than in forests and croplands, and the effects of NH_4NO_3 were greater than those of urea. Pedological factors (soil pH and ammonium), climate (mean annual temperature and aridity index), and N enrichment regimes (rates and types of N enrichment) were dominant modulators of N effects. With increasing rate of N enrichment, the effects of N on most soil nematode parameters shifted from negative in dry and cold climates to positive in wet and warm climates, and from positive to negative with increasing background soil pH. Our spatial prediction identified East Asia, South Asia, and Europe as critical regions where soil nematodes are most negatively affected by current N deposition. These findings suggest that N enrichment has global negative effects on soil nematode communities and food web complexity by soil acidification and NH_4^+ accumulation, which may trigger cascading effects on the entire ecosystem.

Keywords: Nitrogen enrichment, meta-analysis, nematode abundance, nematode ecological indices, environmental factor

1 Introduction

Nematodes comprise ~80% of all terrestrial multicellular animals, with an estimated 4.4 ± 0.64 × 10^{20} individuals inhabiting the upper soil layers worldwide, and store ~0.03 Gt of carbon (C) (Bardgett and van der Putten, 2014; van den Hoogen et al., 2019). These organisms are ubiquitous across all major trophic levels of the soil food web and play critical roles in soil ecosystems. They influence microbial community diversity and structure through top-down regulation, affect soil carbon and nutrient cycling, and impact greenhouse gas emissions (Jiang et al., 2018; Kane et al., 2022; Yeates, 2003). Soil nematode respiration releases ~1.35 Gt of C annually, which is equivalent to 15% of C emissions from fossil fuel use, or 2.2% of total soil C emissions (van den Hoogen et al., 2019). Moreover, soil nematodes were reported to increase N_2O emissions by a range of 53% to 748% (Hu et al., 2024a) and account for up to 40% of nitrogen (N) mineralization in agricultural soils (De Ruiter et al., 1993; Yeates, 2003). They are also closely linked to the structural and functional status of soil food webs (Bongers and Ferris, 1999; Ferris and Matute, 2003) and overall soil health (du Preez et al., 2018; Ugarte et al., 2013; Huang et al., 2024; Li et al., 2025). Thus, examining how the soil nematodes respond to environmental changes is fundamental for comprehensively understanding how terrestrial ecosystems adapt to our changing world (Eisenhauer and Guerra, 2019; van den Hoogen et al., 2019).

Atmospheric deposition of reactive N has increased over the last century, reaching rates as high as 93.6 Tg N yr^{-1} in 2016 (Ackerman et al., 2019), leading to significant N enrichment in terrestrial ecosystems. This excess N input has profoundly altered ecosystem processes and soil communities (Phillips et al., 2024). Nitrogen enrichment significantly increases soil N availability, but causes imbalances or shortages of other essential nutrients such as phosphorus (Xu et al., 2022), shifts plant communities, and acidifies soils (Chen et al., 2015a; Li et al., 2023). These changes impact the abundance, structure, and function of soil nematodes, with studies reporting positive effects in croplands (Jiang et al., 2013b) and grasslands (Hou et al., 2023), negative effects in grasslands (Wei et al., 2012) and forests (Sun et al., 2013), and neutral effects in croplands (Betancur-Corredor et al., 2022) and grasslands (Song et al., 2016). The inconsistent effects may be attributed to variations in environmental conditions like ecosystem types, climates, N forms, and experimental durations, as well as habitat preferences of nematode trophic groups (Gallego-Zamorano et al., 2023; Zhou et al., 2021). Thus, integrating global observational data enables us to elucidate the impacts of N enrichment on soil nematodes across environmental gradients, which is crucial for clarifying the ecological consequences of global N deposition, and for providing a scientific basis in conservation of soil biodiversity in the context of global change.

Existing meta-analyses have examined the response of soil nematodes to N addition, focusing mainly on nematode abundances and diversity (Gallego-Zamorano et al., 2023; Xing et al., 2022b; Zhou et al., 2022). However, there has been little focus on ecological indices (e.g., maturity index, enrichment index and structure index), which are indicative of nutrient cycling efficiency, environmental disturbance, and trophic complexity, and provide critical insights into soil food web dynamics and soil health (Bongers, 1990; Bongers and Bongers, 1998; Yan et al., 2018; Zhang et al., 2024).

The increase in the enrichment index indicates nutrient enrichment, whereas the decreases in the maturity and structure indices indicate environmental disturbance/stress and reduction in soil food web complexity, respectively (Bongers and Ferris., 1999; Ugarte et al., 2013; Ma et al., 2024; Yan et al., 2018). Therefore, this knowledge gap restricts our ability to link N enrichment-induced changes in soil nematodes to broader ecosystem functioning. Furthermore, given that N enrichment rates, climates, biomes, and pedological factors vary significantly across spatial scales and interact with one another (Ackerman et al., 2019; Chen et al., 2023), identifying how these factors combined affect soil nematode communities and their relative importance and potential influence pathways are critical for a global assessment and spatial extrapolation of soil nematode changes in the context of global change.

To address these knowledge gaps, we conducted a global synthesis of field experiments examining the effects of N enrichment (N deposition or addition) on soil nematode communities, using a global dataset of 629 observations from 93 publications (Fig. S1). We aimed to answer the following questions: (1) How do the effects of N on soil nematodes vary with ecosystem types, climates, experimental durations, and forms and rates of N enrichment? (2) What are the key factors influencing N enrichment-induced changes in soil nematodes? (3) What are the spatial patterns of soil nematode community changes in response to N deposition? Our global dataset includes paired N enrichment treatments (i.e., control vs. N enrichment), ecosystem types (cropland, forest, and grassland), climatic regions (tropical and temperate), durations of experiments (short- vs. long-term), and N forms (NH_4NO_3, urea, and organic fertilizer).

To our knowledge, this study provides the most comprehensive global database and estimates of N enrichment effects on various aspects of soil nematode communities.

2 Materials and methods

2.1 Data compilation

Peer-reviewed journal articles that conducted N enrichment experiments and measured indices of soil nematode communities were searched in Web of Science (Core collection; http://apps.webofknowledge.com/) and China National Knowledge Infrastructure (http://www.cnki.net) up to March 2025. The following terms were used, “nitrogen deposition” or “N deposition” or “nitrogen enrichment” or “N enrichment” or “nitrogen addition” or “N addition” or “nitrogen fertili*” or “N fertili*” or “nitrogen amendment” or “N amendment” or “nitrogen input” or “N input” or “nitrogen load*” or “N load*” and “nemat*” or “fauna”. This search resulted in 894 publications.

We screened these publications according to the following criteria: (1) The experiment was conducted under field conditions with both control and N enrichment treatments, excluding laboratory, greenhouse, or pot experiments. (2) Initial environment conditions (i.e., climate, soil, and vegetation) were comparable between control and N enrichment treatments. (3) Experiments combining multiple treatments (e.g., fertilization and tillage) and control (no fertilization and no tillage or no fertilization and tillage) were excluded to avoid any potential confounding effects. (4) The type, rate, and duration of the N enrichment treatment(s) were clearly reported, and could be converted to kg N ha^{-1} yr^{-1}. (5) At least one nematode index (abundance, diversity, or ecological indices) was reported. (6) Only the most recent data were selected, if multiple publications reported similar results from the same experiment. (7) If the results from the same experiment were reported in different publications, only one dataset was retained. (8) Results from different sites within the same publication were considered independent experiments. (9) We focused on the top 0-30 cm depth to avoid the influence of soil depth on N effect. Additionally, focusing on the surface soil layer could capture the most variations in the effects of N enrichment on soil nematodes because this soil layer is the dominant habitats for soil nematodes while the enriched N usually enters this layer (Jones, 1975; Gallego-Zamorano et al., 2023; Hu et al., 2024b). (10) The mean, standard deviation (SD) or error (SE) or coefficient of variation (CV), and sample size of the control and N enrichment treatments could be directly obtained or calculated. We followed the preferred reporting items for meta-analysis (PRISMA) guidelines (Fig. S1) for reviewing, searching, and selecting the dataset. Finally, 629 paired observations from 93 studies were included in our global database (Figs. S1 and S2; Supplementary text S1).

From each publication, we extracted the means, SD, or SE or CV and sample sizes (n) directly from tables, text, and supplementary files or indirectly from graphs using WebPlotDigizer (https://automeris.io/WebPlotDigitizer/). The abundance index included abundances of total nematode and various trophic groups, i.e., plant-feeding nematodes, bacterial-feeding nematodes, fungal-feeding nematodes, and omnivorous-predatory nematodes. We also used the nematode diversity index. The ecological indices included the enrichment index, maturity index, and structure index of soil nematodes. We consistently collected data on genus diversity of nematode communities, considering that nematode taxa at the genus and family levels are the most effective units (Bongers and Bongers, 1998; Gallego-Zamorano et al., 2023), and studies often reported nematode diversity at the genus level. When only the relative abundance of each trophic group and the total abundance of nematodes were reported, we back-calculated the absolute abundance of the nematode groups (individuals per 100 g dry soil).

We also recorded information on geographic location, experimental design (i.e., rate of N enrichment, duration of the experiment, type of N fertilizer), and ecosystem type from each selected publication. Ecosystems were categorized into three types: forest, grassland, and cropland. The N fertilizer types were categorized into NH_4NO_3, urea, organic fertilizer, and other sources based on the authors' information. We also collected other ancillary data, including mean annual temperature (MAT), mean annual precipitation (MAP) (if not reported, estimated using WorldClim), aridity index (AI) (estimated using Global Aridity and Potential Evapotranspiration Database), soil organic carbon (SOC), total nitrogen (TN), soil pH, soil mineral N (NH_4^+ and NO_3^-), and soil texture (sand, silt, and clay percentages, estimated using SoilGrids250m 2.0 if not reported). When some values of ancillary data were not reported, we searched other articles from the same site by the same authors and institutes to obtain the corresponding ancillary data. Overall, our global dataset included studies from North America, South America, Asia, Europe, Africa, and Oceania, and has a wide range of N enrichment rates (up to 600 kg N ha^{-1} year^{-1}), experiment duration (up to 32 years), MAP (175 to 1945 mm), and MAT (-5.8 to 27.5°C); thus, it can comprehensively illustrate the response of soil nematodes to N enrichment across global ecosystems and climates.

2.2 Effect size calculation

We calculated the effect size of N enrichment as the natural logarithm of the response ratio (*lnRR*). The *lnRR* is effective in reducing the heteroscedasticity of data and has advantages in dealing with proportional data and the assumption of a normal distribution, which is less prone to statistical artefacts associated with ratio-based regressions (Benítez-López et al., 2021). We calculated bias-corrected effect sizes ($lnRR^{\Delta}$) based on the Delta method to account for the small sample size bias (Lajeunesse, 2015):

$$lnRR^{\Delta} = \ln\left(\frac{X_t}{X_c}\right) + \frac{1}{2}\left(\frac{SD_t^2}{n_t X_t^2} - \frac{SD_c^2}{n_c X_c^2}\right)$$

where X_t and X_c are the mean values of variables in the N enrichment and control treatments, respectively. SD_t and SD_c are the standard deviations of the N enrichment and control treatments, and n_t and n_c are the number of replicates of the N enrichment and control treatments, respectively. For each $lnRR^{\Delta}$, the corresponding sampling variance $VAR(lnRR^{\Delta})$ (Lajeunesse, 2015; Gallego-Zamorano et al., 2023), calculated as follows:

$$VAR(lnRR^{\Delta}) = \frac{SD_t^2}{n_t X_t^2} + \frac{SD_c^2}{n_c X_c^2} + \frac{1}{2}(\frac{SD_t^4}{n_t^2 X_t^4} + \frac{SD_c^4}{n_c^2 X_c^4})$$

In our dataset, some of the included studies only reported the standard errors (SE);

we then calculated the SD according to the equation as below:

$$\mathrm{SD} = \mathrm{SE} \times \sqrt{n}$$

When the *SD* or *SE* were not reported in publications, we imputed the SDs based on the coefficient of variation from all complete cases using the impute_SD function from the R package metagear (Bracken, 1992).

2.3 Meta-analysis

Random-effects meta-analysis without any moderators (intercept-only models) was performed to estimate the overall mean effect size of N enrichment on soil nematode indices. We fully accounted for non-independence among effect sizes through the following settings. Firstly, the study identity and unit-level observation identity were set as random effects to account for possible autocorrelations among observations and residual variance in each study, respectively. Secondly, as multiple treatments were often compared with a single control (i.e., shared control), we accounted for these repeated measures in a variance-covariance matrix, where the diagonal includes the sampling variances and the off-diagonals of the matrix represent the shared variance (covariance) among the effect sizes due to the common control (Lajeunesse, 2011):

$$COVAR(lnRR^{\Delta}) = \frac{SD_c^2}{n_c X_c^2} + \frac{1}{2}(\frac{SD_c^4}{n_c^2 X_c^4})$$

Finally, we also intended to account for phylogenetic non-independence of nematode communities. However, the majority of publications lacked any phylogenetic information on nematode communities, and the phylogeny of nematodes remains unresolved (Kern et al., 2020). Therefore, we were unable to control for the non-independence of taxonomy in the models of nematode communities, which needs to be considered in future studies. We then partitioned each random effect by providing Q as a measure of total absolute heterogeneity and I^2 as a measure of total relative heterogeneity (Table S1; Nakagawa and Santos, 2012).

To investigate the sources of heterogeneity observed in the intercept-only model, we characterized the role of several moderators (i.e., ecosystem type and N fertilizer type) by employing meta-analytic models with the same random-effects structure as the intercept-only model. We employed restricted maximum likelihood estimation to fit the above models and to calculate the weighted effect sizes and 95% confidence intervals (CI) using rma.mv function in the *metafor* package (Viechtbauer, 2010). The effect of N enrichment was considered significantly positive ($lnRR^{\Delta} > 0$, $P < 0.05$) or negative ($lnRR^{\Delta} < 0$, $P < 0.05$) if the 95% CIs did not overlap with zero. The omnibus test (Q_M) was then used to evaluate the significance of the categorical moderators in the mixed-effects models. We performed post-hoc tests for categorical moderators using the linearHypothesis function in the *car* package.

2.4 Meta-regression

Multiple meta-regression models were employed to evaluate the effects of N enrichment ($lnRR^{\Delta}$) on soil nematode indices as influenced by potential moderators, including rates and duration of N enrichment, soil and climate data. We conducted the meta-regression analysis using the rma.mv function in the *metafor* package

(Viechtbauer, 2010), and also accounted for non-independence among effect sizes in the models by setting up the same random-effects structure as in the above-mentioned intercept-only and mixed models. We then extracted model slope estimates and predicted values to visualize the graphs.

In addition, considering that rate of N enrichment could potentially be key indicator of N enrichment experiments, and that heterogeneity of soil, climate, ecosystems, and fertilizer types in real-world scenarios may influence the potential effects of different N enrichment rates, we analyzed interaction effects between rate of N enrichment and each of the moderators in the multiple meta-regression models. The continuous variables were represented as quantile values of 5%, 25%, 50%, 75%, and 95% for each moderator. The Q_M was then used to assess the significance of the interaction between N enrichment rate and moderators.

2.5 Robustness test

We performed a series of analyses to ensure the robustness of the results. Firstly, we calculated bias-corrected effect sizes ($lnRR^{\Delta}$) based on the delta method to account for the small sample size bias (Lajeunesse, 2015), and compared these and uncorrected *lnRR* (Fig. S3). Secondly, the funnel plot analysis was conducted to assess the publication bias, and the asymmetry of the funnel plot was evaluated by Egger's regression test (Egger et al., 1997). If asymmetry was detected, the Rosenberg fail-safe number was used to further determine whether the the potential for publication bias affected our results (Rosenberg, 2005). Thirdly, we tested for small-study bias by running meta-analytic models with either standard error (square root of VAR($lnRR^{\Delta}$)) or the inverse of effective sample size as the only moderator. Fourthly, we performed meta-regression models with publication year as the only moderator to assess the time-lag effects, that is, whether statistically significant or larger effect sizes were published earlier than nonsignificant or smaller effect sizes. Finally, we evaluated the sensitivity analysis of results by performing leave-one-out analysis.

We found that the funnel plots were symmetric ($P > 0.05$) for most nematode parameters (except for the enrichment index), and the Rosenberg fail-safe numbers for these all metrics were much larger than 5k+10 (Fig. S4 and Table S2). In addition, the responses of most soil nematode parameters to N enrichment were not clearly associated with standard error (Fig. S5), the inverse of effective sample size (Fig. S6), and publication year (Fig. S7, $P > 0.05$). Furthermore, the leave-one-out analysis suggested our results are unlikely to be driven by a single influential observation and study by removing any observation or study (Figs. S8 and S9). Collectively, there was no evidence of publication bias for soil nematodes parameters in response to N enrichment. All of these analyses suggest that our results were robust.

2.6 Statistical analyses

We conducted a model-selection analysis to examine the relative importance of each individual moderator by analyzing possible combinations of the moderators considered in mixed-effects meta-regression models using the *metafor* (Viechtbauer, 2010) and *glmulti* packages (Calcagno and de Mazancourt, 2010). The relative importance for each moderator was calculated as the sum of the Akaike weights, with larger values indicating greater contributions. A threshold value of 0.8 was set to distinguish between essential and non-essential moderators.

To evaluate the direct and indirect pathways of climate heterogeneity and the response of soil variables in influencing the effects of N on soil nematodes, we conducted piecewise structural equation modelling (SEM) incorporating rates and duration of N enrichment, climatic factors (MAT and aridity index), and $lnRR^{\Delta}$ of soil variables (SOC, TN, NH_4^+, NO_3^-, and pH) based on the above results of the relative importance of the moderators. An *a priori* conceptual model was established to depict the potential paths and its ecological significance (Table S3; Fig. S10). Each component model of the piecewise SEM was fitted as a linear mixed model, with the aforementioned variables as fixed effects, the study nested within observation IDs as random effects. All the variables were standardized for the effects to be directly comparable (Mhlanga et al., 2022). The models were modified by removing nonsignificant direct and indirect paths to achieve a lower Akaike information criterion (AIC) when the initial models did not produce any adequate fit. The Shipley's d-separation test was used to examine whether any paths were missing from the model (Shipley, 2013). We constructed the SEM and reported the standardized coefficient for each path from each component model, and the Fisher's C statistics and P value ($P >$ 0.05 indicated an adequate model fit) by using the *piecewiseSEM* and *nlme* packages (Lefcheck and Freckleton, 2015; Pinheiro et al., 2018). Given that the effects of N enrichment may be modulated by climate factors and duration on a global scale, we further examined the results with a new SEM model including interaction effects. We found that the new model only affected the magnitude of the path coefficients, without influencing their significance or direction (Fig. S11). We therefore reported the results from the SEM model without interaction effects in the main text.

To reveal spatial patterns of changes in soil nematode abundances under N deposition, we projected the predictions of the model onto raster maps based on maps of global N deposition rates (Fig. S12 and Table S4; Ackerman et al., 2019), and maps of soil variables (Table S4; Poggio et al., 2021) as well as maps of climate (Table S4; Fick and Hijmans, 2017). Given that most publications included in our dataset locates in Northern Hemisphere, we only predicted the spatial patterns of N effect in Northern Hemisphere rather than the whole global pattern to minimize the uncertainties due to the geographic bias of publications. The boosted regression tree (BRT) models were used to perform predictions and extrapolate, which is a machine-learning method based on multivariable regression trees and a boosting technique to improve performance of multiple single models (Elith et al., 2008). We selected the BRT models, because it can effectively deal with the complex variable interactions, identify nonlinear relationships between response variables and their predictor factors, thus avoiding overfitting, and they have been used successfully in previous global synthesis studies (Cao et al., 2023; Graco-Roza et al., 2022; Lin et al., 2024). Given the intrinsic stochasticity of BRT modeling, the measures of variable importance and predictions based on the model may be sensitive to random changes in the number of seeds and differ between runs. To account for this variability, we ran 100 iterations of the models with a series of tuning parameters including n.trees, interaction.depth, and shrinkage. Additionally, we implemented 10-fold cross-validation and bag fraction of 0.75, following a previous study (Elith et al., 2008). The optimal parameter settings were determined based on minimizing RSME, followed by rerunning the model to obtain the final predictive model. The BRT models were constructed using the train function in the *caret* package (Kuhn, 2008). However, due to significant loss of statistical power in the predictive models for soil nematode diversity and ecological indices, we refrained from conducting any spatial extrapolation predictions (Table S5). Consequently, we opted to only perform extrapolation predictions for the models of abundance of total nematodes and different nematode trophic groups. Prior to spatial analyses, we performed Moran's I test by using spdep package to determine whether spatial autocorrelation could affect our models. We found the Moran’s I statistic ranges between -0.15 and -0.05 ($P =$ 0.8722 to 0.9999), indicating non-significant spatial autocorrelation in our data (Table S6). We therefore did not consider spatial autocorrelation when predicting spatial patterns. To assess the uncertainties of spatial prediction, we firstly performed 100 iterations of bootstrap resampling and compared the results to the original prediction maps, and calculated the coefficient of variation (CV) of averaged predictions and 95% confidence intervals. Our assessment showed that the spatial prediction had relatively generally lower uncertainties, but higher in certain sparsely sampled regions such as Central Asia and the southern Sahara Desert (Figs. S13 and S14).

In addition, to assist in validating the direction of global N deposition on the abundance of soil nematodes, we spatially overlaid the raster maps of global nematode abundance (Fig. S15; van den Hoogen et al., 2019) and the raster map of global N deposition rates (Fig. S12; Ackerman et al., 2019) to re-project them to the same resolution and to analyze the linear or nonlinear relationship between rates of global N deposition and nematode abundance of total and trophic groups by using linear, quadratic, and generalized additive models. This allowed us to determine the effects of N on the abundance of total soil nematodes and different trophic groups from an alternative perspective at the global scale.

3 Results

3.1 Effects of N enrichment on the soil nematode community

Our meta-analysis revealed that N enrichment significantly decreased the abundance of omnivorous-predatory nematodes (-28.3%, $P < 0.01$, Fig. 1). In contrast, it had minimal effects on the abundance of total nematodes (-4.6%, $P > 0.05$) and other nematode trophic groups (-11.9% to +9.8%, $P > 0.05$). Additionally, N enrichment significantly reduced the Shannon diversity index (-3.2%, $P < 0.01$), maturity index (-6.1%, $P < 0.01$), and structure index (-12.3%, $P < 0.01$), but had minimal impact on the enrichment index (-0.2%, $P > 0.05$, Fig. 1).

Within different ecosystems, N enrichment significantly reduced the abundance of total nematodes (-13.3%, $P < 0.05$), fungal-feeding nematodes (-29.4%, $P < 0.01$), and omnivorous-predatory nematodes (-39.0%, $P < 0.01$) in grasslands. It increased the abundance of bacterial-feeding nematodes (20.7%, $P < 0.05$) in croplands (Fig. 1; Tables S7 and S8), but had no significant effect on plant-feeding nematodes across ecosystems ($P > 0.05$). N enrichment decreased nematode diversity in grasslands (-4.8%, $P < 0.01$), maturity index in grasslands (-8.7%, $P < 0.01$) and croplands (-4.6%, $P < 0.05$), and structure index in forests (-13.6%, $P < 0.01$) and croplands (-18.1%, $P < 0.05$), while the enrichment index remained unaffected ($P > 0.05$, Fig. 1; Tables S7 and S8).

Regarding N input types, NH_4NO_3 significantly reduced the abundance of plant-feeding nematodes (-16.7%, $P < 0.01$), fungal-feeding nematodes (-25.7%, $P < 0.01$), and omnivorous-predatory nematodes (-36.4%, $P < 0.01$). In contrast, organic N (e.g., manure) significantly increased the abundance of total nematodes (+79.9%, $P < 0.01$), plant-feeding nematodes (+96.5%, $P < 0.01$), fungal-feeding nematodes (+132.7%, $P < 0.01$), and bacterial-feeding nematodes (+177.8%, $P < 0.01$, Fig. 1; Tables S9 and S10). Nematode diversity (-3.4%, $P < 0.05$) and ecological indices (-5.9% to -10.1%, $P < 0.05$) were significantly reduced by urea and NH_4NO_3, but were not significantly affected by organic N ($P > 0.05$, Fig. 1; Tables S9 and S10).

3.2 Factors modulating the effects of N enrichment

The effects of N on most soil nematode indices were significantly negatively correlated with the rates of N enrichment ($P < 0.05$, Fig. S16) and changes in soil NH_4^+ ($P < 0.05$, Fig. S17). Conversely, they were significantly positively correlated with MAT ($P < 0.05$), aridity index ($P < 0.05$), and changes in soil pH ($P < 0.01$, Fig. S16). The N enrichment rate and climatic conditions had a more pronounced impact on fungal-feeding and omnivorous-predatory nematodes compared to plant-feeding and bacterial-feeding nematodes, and influenced nematode diversity and enrichment index more than the structure index and maturity index (Fig. S16).

Multilevel meta-regression models indicated that the relationships between soil nematodes and N enrichment rate were moderated by climatic and soil pH conditions ($P < 0.05$ for the interaction, Fig. 2). The abundance of most groups of soil nematodes, diversity, and enrichment index generally decreased with increasing N enrichment rates in dry and cold climates, but increased in wet and warm climates ($P < 0.05$ for the interaction, Fig. 2a, b). The effects of N enrichment rates on nematode abundance and diversity shifted from positive to negative with increasing background soil pH ($P < 0.05$ for the interaction, Fig. 2c). However, the impact of N enrichment rates on most nematode indices (except omnivorous-predatory nematode abundance) was not significantly influenced by experiment duration ($P > 0.05$ for the interaction, Fig. 2d). These results highlight the critical role of climate and soil pH in modulating nematode responses to N enrichment rates.

Importantly, model selection analyses further showed that N effects on soil nematodes were largely explained by changes in pedological factors (soil pH, NH_4^+, and SOC), and were modulated by climate (MAT and aridity index) and N enrichment regimes (rates and types of N enrichment) (Fig. 3). The SEM based on these key factors revealed that N enrichment primarily impacted soil nematode communities by decreasing soil pH and increasing soil mineral N (especially NH_4^+), which in turn reduced nematode abundance, diversity, enrichment index and structure index (Fig. 4). Longer experimental duration exacerbated the negative effects of N by enhancing soil pH reduction. Large-scale climatic variations had limited direct effects, but they indirectly influenced N enrichment-induced changes in soil nematodes via altering pedological factors (Fig. 4).

3.3 Spatial patterns of soil nematode responses to current N deposition

Extrapolating N enrichment-induced changes in soil nematode abundance at the Northern Hemisphere scale using atmospheric N deposition, soil, and climate raster data revealed significant spatial variation (Fig. 5). Negative effects of N deposition were most pronounced in regions of East Asia, South Asia, and Europe, which correspond to the higher atmospheric N deposition levels in these regions (Figs. 5 and S12). Spatial raster overlay analysis of global nematode abundance and N deposition maps showed that the abundances of total nematodes and trophic groups decreased progressively with increasing global N deposition rates (Fig. 5f-j). Conversely, N deposition resulted in slight increases in soil nematode abundances in low-latitude/equatorial regions characterized by hot and humid climates. The negative impacts of N deposition were more significant on omnivorous-predatory and fungal-feeding nematodes compared to bacterial-feeding nematodes, and such effects tended to be amplified when N availability increased (Fig. 5).

4 Discussion

The present comprehensive meta-study on the most abundant Metazoans on Earth shows that N enrichment has global negative effects on soil nematode communities by decreasing nematode diversity and soil food web complexity. Moreover, we show significant differences among trophic groups in their responses to N enrichment, and that such effects are further modulated by climatic and soil conditions. Importantly, we identify underlying mechanisms of changes in soil nematode communities (soil acidification and NH_4^+ accumulation) and identify global vulnerable areas that should be in the focus of nature protection and potential counter-measures against the ecosystem consequences of N enrichment.

4.1 Overall effects of N enrichment on soil nematodes

The negative effects of N on soil nematode communities were primarily due to the N enrichment-induced soil acidification and NH_4^+ accumulation (Figs. 4, S16~S19). Soil acidification not only reduced the availability of base mineral cations (Ca^{2+} and Mg^{2+}) (Chen et al., 2015a; Lucas et al., 2011; Tian and Niu, 2015; Tibbett et al., 2019), which resulted in deficiencies of nutrients to nematodes and other organisms, but also increased soil acid cations (H^+ and Al^{3+}) and thus enhanced the toxicity of these cations to nematodes (Chen et al., 2015a; Tibbett et al., 2019), both resulting in a reduction of nematode diversity and abundance. Additionally, soil acidification has been shown to reduce soil microbial biomass (Chen et al., 2015a; Zhang et al., 2018), which indirectly decreased nematode abundance and diversity via reduced resource availability to a variety of nematode trophic groups (e.g., bacterial-feeding, fungal-feeding, and omnivorous-predatory nematodes) (Eisenhauer et al., 2013; Ferris, 2010). This N-induced variation in soil nematode communities may weaken ecosystem stability. For example, N enrichment significantly reduced the maturity and structural indices (Fig. 1), which were indicative of increased environmental disturbances/stresses and reduced soil food web complexity (Bongers and Ferris, 1999; Ugarte et al., 2013; Yan et al., 2018; Ma et al., 2024).

In this study, we provided global evidence that the N enrichment-induced changes in nematode abundances differed among trophic groups (Fig. 1). N enrichment significantly increased plant biomass, root C, or rhizodeposition (Feng et al., 2023; Chen et al., 2015a), which would have positive effects on plant-feeding nematodes (Keith et al., 2009). However, N enrichment may lead to negative effects on abundance of plant-feeding nematodes due to NH_4^+ suppression (Wei et al., 2012), and such a negative effect was supported by the NH_4NO_3-induced significant decrease in the abundance of plant-feeding nematodes in the present meta-study (Fig. 1). Plants could take up abundant soil NH_4^+ and its high concentrations could kill plant-feeding nematodes potentially through the dissociation of NH_4^+ ions into toxic ammonia (NH_3), and by altering the osmotic potential within plant tissues and soil solution (Tenuta and Ferris, 2004). Moreover, current studies demonstrated that high soil NH_4^+ concentrations were toxic to plants through rhizosphere acidification due to protons (e.g., H^+) excretion and suppression of cation uptake (Li et al., 2014), which may be unfavorable to plant-feeding nematodes. Such negative impacts of soil NH_4^+ suppression intensified with increasing N enrichment rates in the present study (Figs. S16 and S20), and thus may exceed the positive effect of root biomass on the abundance of plant-feeding nematodes.

We found that the higher trophic-level omnivorous-predatory nematodes were more susceptible to N enrichment-induced high NH_4^+ concentrations and low soil pH (Figs. 1, S16 and S17; Puissant et al., 2021; Chen et al., 2025a), likely due to the less developed cuticle structure and secretory-excretory systems, which resulted in reduced osmoregulatory capacity (Tenuta and Ferris, 2004). More importantly, compared with other nematode trophic groups, omnivorous-predatory nematodes typically have longer life spans and lower reproduction rates, resulting in a lower ability to recover from environmental stress (Bongers, 1990; Bongers and Bongers, 1998). Furthermore, N enrichment may shift soil food composition from fungi-dominated to bacteria-dominated, thereby reducing the abundance and diversity of fungi (Treseder, 2008; Shaw et al., 2019) and thus the abundance of fungal-feeding nematodes. The majority of bacterial-feeding nematodes are r-strategists characterized as fast-growing phenotypes, which recovered more readily from environmental stress (Shaw et al., 2019). Such shifts in soil energy channels may indicate significant alterations of soil conditions and service provisioning (de Vries et al., 2013).

4.2 Climate regulates effects of N enrichment on soil nematodes

We found that N enrichment-induced changes in soil nematodes were significantly positively correlated with mean annual temperature and aridity index (Figs. 2 and S16), primarily because the limitation of moisture and temperature resulted in lower ecosystem N requirements in dry or cold regions than in wet or warm conditions (Del Grosso et al., 2008; Lie et al., 2020; Xing et al., 2022b). Dry or cold regions were more susceptible to N saturation (Xing et al., 2022b), and weaker N-induced NH_4^+ accumulation and stronger soil acidification (Fig. S21) under current N deposition rates. However, warm and humid regions showed an opposite pattern (Fig. S21). Additionally, soil nematodes live in the water film of soil pores, and their movement is thus critically determined by soil moisture (Jones, 1975; Xiong et al., 2021). Wet or warm conditions are more conducive to nutrient solubilization, nematode migration and predation, contributing to the positive effects of N on nematode diversity and abundance (Xing et al., 2022b), explaining our results that N enrichment increased nematode abundance and diversity in warm and humid regions (e.g., equatorial regions) (Fig. 5). Therefore, drought and cold conditions exacerbated the negative effects of N on soil nematodes, and this impact could be further intensified by increasing N enrichment rates (Figs. 2 and S16). We hence predict that future N enrichment may simplify soil food webs in arid and cold regions but may contribute to higher soil food web complexity in humid and warm regions (Gallego-Zamorano et al., 2023; Xing et al., 2022b), as long as soil moisture levels are sufficiently high.

4.3 Variations in the effects of N enrichment across ecosystems

We found more negative effects of N enrichment on soil nematodes in grassland than in cropland and forest, which could be ascribed to several reasons. Firstly, the N enrichment-induced reduction of soil pH and increase in soil mineral N (NH_4^+ and NO_3^-) concentrations were stronger in grassland than in forest (Fig. S19b), resulting in stronger negative effects on nematodes in grassland. Although such effects of N enrichment on soil pH and mineral N were also stronger in cropland, the more frequent anthropogenic disturbances such as fertilization and tillage may enhance the tolerance of nematode communities to additional N inputs (Zhou et al., 2021), which may mitigate the detrimental effects of pH and mineral N on soil nematodes. Secondly, N enrichment usually decreases the concentrations of soil base mineral cations (Ca^{2+}, Mg^{2+}, and K^{+}), which not only exacerbates soil acidification, but also impacts plant growth (Chen et al., 2015a; 2015b). Such an N enrichment-induced depletion of soil base mineral cations is usually greater in grasslands than in other ecosystems (Tian and Niu, 2015), possibly indirectly contributing to the more negative impacts of N on soil nematodes. Thirdly, grasslands generally had drier (525 vs. 1016 and 853 mm) and colder (4.41 vs. 13.94 and 11.13°C) climatic conditions than forests or croplands in our dataset, which may intensify the negative effects of N on soil nematodes as suggested by our result that drought and cold conditions exacerbated the negative effects of N on soil nematodes (Figs. 2 and S16; Gallego-Zamorano et al., 2023). Collectively, soil nematode communities are more vulnerable in response to N in grassland, and thus practices mitigating negative effects of N should be particularly focused on this ecosystem type, particularly in dry and cold climatic regionns.

4.4 Effects of N enrichment depend on the types and amounnts of N inputs

We showed that effects of N on soil nematodes intensified with increasing rates of N enrichment (Figs. 2 and S16), mainly because the excess N availability overwhelmed the N demand of soil nematodes, resulting in adverse effects on their abundance and diversity. Moreover, such effects were more pronounced for the higher trophic levels of nematodes (fungal-feeding and omnivorous-predatory nematodes), mainly because these nematode populations are more sensitive to disturbances and require more time to recover than faster-growing bacterial-feeding nematodes (Ferris et al., 2001; Xing et al., 2022b).

We demonstrated that NH_4NO_3 had greater negative effects on soil nematodes than urea (Fig. 1), primarily due to the direct toxicity of NH_4^+ or the acidification from H^+ release during NH_4^+ uptake and nitrification, whereas the slower release and transformation of urea ($CO(NH_2)_2$) may lessen these negative effects, thereby reduced nematode diversity and the abundance of plant-feeding, fungal-feeding, and omnivorous-predatory nematodes (Puissant et al., 2021; Zhou et al., 2021). On the contrary, we found that organic N significantly increased the abundance of total soil nematodes and trophic groups, but did not affect the diversity and ecological indices (Fig. 1), probably because organic N had only minor effects on soil pH (Fig. S19), but supplies nutrients and microbial food sources for soil nematodes to promote reproduction (Fig. S19; Jiang et al., 2013a; Liu et al., 2016). These results were in line with global meta-analyses of many groups of soil animals (Beaumelle et al., 2020; Phillips et al., 2024) and highlighted that we may be able to effectively manage soil nematode communities by adapting management strategies, such as preferring organic over mineral fertilizer applications (Liu et al., 2016; Puissant et al., 2021). However, it is important to note that there were relatively few observations of organic N treatments in this meta-analysis, which may affect the robustness of the results and need to be interpreted with caution. Future studies should focus on organic N treatment and acquire more comprehensive experimental data on soil nematode responded to organic N inputs.

4.5 Spatial patterns of soil nematode responses to current N deposition

By investigating spatial response patterns of soil nematodes to N enrichment, we found more negative responses of soil nematodes in East Asia, South Asia, and Europe, corresponding to the higher N deposition rates (Ackerman et al., 2019) and greater reductions in soil pH (Chen et al., 2023) in these regions. We also predicted a negative effect in boreal forest, tundra, or desert regions (Fig. S22). The ecosystems in these regions are often restricted by water availability or temperature (Bradford et al., 2020; Paroshy et al., 2021). Soil nematodes live in the water film of soil pores, and their movement and predation are thus determined by soil moisture (Jones, 1975; Neher, 2010; Xiong et al., 2021). Wet conditions are more conducive to nutrient solubilization, nematode migration and predation (Xiong et al., 2020; 2021), thus contributing to the positive effects of N on nematode diversity and abundance (Xing et al., 2022b). In addition, more rainfall in wet region also prevented excessive accumulation of toxic N compounds by leaching (Fig. S21; Cui et al., 2022; Gallego-Zamorano et al., 2023), and the N-induced soil acidification was less pronounced (Fig. S21). Previous studies demonstrated that drought amplified the negative effects of N enrichment on abundance of soil nematodes (Wang et al., 2021; Gallego-Zamorano et al., 2023), whereas increased precipitation transformed these negative effects into positive effects

(Martinez et al., 2023).

Additionally, low temperatures in cold regions constrained soil microbial activity and resulted in lower N demands, which led to them being more susceptible to N saturation (Fig. S21; Xing et al., 2022b) and stronger N-induced soil acidification (Fig. S21) under current N deposition. These were detrimental to growth and activity of soil nematode. Previous study also showed that high levels of N addition reduced soil microbial biomass and activities in cold boreal forests (Xing et al., 2022a), which may reduce food sources for soil nematodes. Additionally, the effect of N on soil microbial biomass was reported to be more negative in cold than in warm climates (Zhang et al., 2018), which may further decrease the abundance of microbial-feeding soil nematodes in these regions. On the contrary, we predicted increased soil nematode abundances in temperate systems and tropical rainforests under current N deposition scenarios (Fig. 5), which was consistent with our results that N enrichment increased nematode abundance and diversity in warm and humid regions (e.g., equatorial regions) (Figs. 2, 5 and S16). Overall, our assessment emphasized the significant spatial heterogeneity in the responses of soil nematodes to current levels of global N deposition, which should be carefully considered when assessing and predicting the spatial patterns of soil nematode communities and functionality in a changing world.

4.6 Management implications

Because the impacts of N enrichment on soil nematodes may be largely mediated by "bottom-up" effects from soil, plants, and microbes (Mueller et al., 2016; Tian et al., 2024), the effects of N enrichment on soil nematodes may propagate through the soil food web and trigger cascading effects on the entire ecosystem (Eisenhauer et al., 2012; 2013). To mitigate these negative effects of N enrichment, our findings suggest the following potential solutions:

(1) Developing regional management schemes to reduce excessive N emissions. Strict N emissions regulations should be implemented in regions with severe N deposition, such as East Asia, South Asia, and Europe. The low-N combustion and waste gas treatment technologies could be promoted to reduce N oxide emissions.

(2) Optimizing fertilization technologies. The organic fertilizers or slow-release fertilizers could be prioritized as substitutes for chemical N fertilizers so as to minimize the effects of N on soil nematodes. The lime could be co-applied with N fertilizers to mitigate N-induced soil acidification.

(3) Restoring degraded ecosystems. Vegetation and ecological restoration in degraded and fragile regions could enhance input of soil organic matter and buffering capacity and improve soil structure, which could offer a more favorable environment for soil nematodes.

(4) Developing policy-driven incentives. The ecological index of soil nematode could be incorporated into the assessment system for land degradation and soil health. The policy-based subsidies could be awarded to farmers who adopt organic fertilizers, slow-release fertilizers or precision fertilization techniques.

4.7 Limitations and future perspectives

In this study, we compiled a global database to examine the effects of N enrichment on soil nematodes, whereas 94% and 6% observations located in Northern and Southern Hemispheres, respectively. Such geographic bias limited the application of our meta-analysis in Southern Hemisphere, highlighting that experimental studies should be further concentrated in such region. Additionally, almost all environmental variables, which were essential for upscaling of the N effect, were not fully reported. Extracting such data from the global raster dataset may result in additional uncertainty to the analyses. Modelling uncertainty due to this should also be considered when constructing projections of a variable in response to a global change factor.

Generally, N enrichment has potential synergistic impacts with other global change factors (Niu et al., 2020). For example, drought amplified while other nutrients (e.g., phosphorus) enrichment ameliorated the negative effects of N enrichment on soil nematodes (Wang et al., 2021; Gallego-Zamorano et al., 2023; Ma et al., 2024). Future research should focus on the combined effects of such factors with N enrichment to better predict soil community changes and their broader impacts on terrestrial ecosystems. Moreover, bridging plants, soil microbes, and nematodes will help us predict ecosystem functions better under global changes. Such efforts should include integrating the currently proposed plant economics spectrum (Reich, 2014), microbial life strategy histories (Malik et al., 2020), and nematode economics spectrum (Zhang et al., 2024).

5 Concluding remark

This study provided a comprehensive understanding of how global N enrichment affected soil nematodes by demonstrating that: (1) N enrichment significantly decreased soil nematode abundance, diversity, and ecological indices; (2) these negative effects were more pronounced in grasslands than in forests and croplands, and with application of NH_4NO_3 than with that of urea; (3) with increasing rate of N enrichment, the effects of N shifted from negative in dry and cold climates to positive in wet and warm climates, and from positive to negative with increasing background soil pH; (4) soil pH and ammonium accumulation explained the response of nematodes to N enrichment; and (5) regions in East Asia, South Asia, and Europe were most negatively affected by current N deposition rates. Given the significant role of soil nematodes in nutrient cycling and ecosystem function (Schloter et al., 2003; Jiang et al., 2018; van den Hoogen et al., 2019; Zhang et al., 2024), the findings presented herein merit integration into global biogeochemical models.

Acknowledgements

This study was supported, in part, by the National Natural Science Foundation of China (42277349, 42407469 and 42307453), the National Key Research and Development Program (2022YFF1302800), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB40020000), the Young Talent Fund of Association for Science and Technology in Shaanxi, China (20240631) and the German Research Foundation (DFG - FZT 118, 202548816), as well as the DFG (Ei 862/29-1; Ei 862/31-1).

Conflict of interest

The authors declare no competing interests.

Author contributions

X.W. conceived this project. J.J., Y.S., X.G., and W.K. collected data. W.K., and X.W. analyzed the results and wrote the first draft of the manuscript, and N.E., J.P., L.Q., M.S., X.J., X.W., and G.W. contributed to subsequent revisions. All authors contributed to the final written product.

Data availability statement

The data that support the findings of this study are available in the Figshare repository at https://doi.org/10.6084/m9.figshare.27798195.

References

Ackerman, D., Millet, D.B., Chen, X., 2019. Global estimates of inorganic nitrogen deposition across four decades. Glob. Biogeochem. Cycles 33, 100-107. https://doi.org/10.1029/2018GB005990

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505-511. https://doi.org/10.1038/nature13855

Beaumelle, L., De Laender, F., Eisenhauer, N., 2020. Biodiversity mediates the effects of stressors but not nutrients on litter decomposition. Elife 9, e5565. https://doi.org/10.7554/eLife.55659

Benítez-López, A., Santini, L., Gallego-Zamorano, J., Milá, B., Walkden, P., Huijbregts, M.A.J., Tobias, J.A., 2021. The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. Nat. Ecol. Evol. 5, 768-786. https://doi.org/10.1038/s41559-021-01426-y

Betancur-Corredor, B., Lang, B., Russell, D.J., 2022. Organic nitrogen fertilization benefits selected soil fauna in global agroecosystems. Biol. Fertil. Soils 59, 1-16. https://doi.org/10.1007/s00374-022-01677-2

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14-19. https://doi.org/10.1007/BF00324627

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239-251. https://doi.org/10.1016/S0929-1393(98)00123-1

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Evol. Ecol. 14, 224-228. https://doi.org/10.1016/S0169-5347(98)01583-3

Bracken, M.B., 1992. Statistical methods for analysis of effects of treatment in overviews of randomized trials, In Sinclair, J.C., Bracken, B.M. (Eds.), Effective care of the newborn infant. Oxford University Press., pp. 13-20.

Bradford, J.B., Schlaepfer, D.R., Lauenroth, W.K., Palmquist, K.A., 2020. Robust ecological drought projections for drylands in the 21st century. Glob. Change Biol. 26, 3906-3919. https://doi.org/10.1111/gcb.15075

Calcagno, V., de Mazancourt, C., 2010. glmulti: An R package for easy automated model selection with (generalized) linear models. J. Stat. Softw. 34, 1-29. https://doi.org/10.18637/jss.v034.i12

Cao, Y., Ding, J., Li, J., Xin, Z., Ren, S., Wang, T., 2023. Necromass-derived soil organic carbon and its drivers at the global scale. Soil Biol. Biochem. 181, 109025.

https://doi.org/10.1016/j.soilbio.2023.109025

Chen, C., Xiao, W., Chen, H.Y.H., 2023. Mapping global soil acidification under N deposition. Glob. Change Biol. 29, 4652-4661. https://doi.org/10.1111/gcb.16813

Chen, D. Lan, Z. Hu, S., Bai Y., 2015a. Effects of nitrogen enrichment on belowground communities in grassland: Relative role of soil nitrogen availability vs. soil acidification. Soil Biol. Biochem. 89, 99-108. https://doi.org/10.1016/j.soilbio.2015.06.028

Chen, D., Li, J., Lan, Z., Hu, S., Bai, Y., Niu, S., 2015b. Soil acidification exerts a greater control on soil respiration than soil nitrogen availability in grasslands subjected to long-term nitrogen enrichment. Funct. Ecol. 30, 658-669. https://doi.org/10.1111/1365-2435.12525

Cui, S., Han, X., Xiao, Y., Wu, P., Zhang, S., Abid, A., Zheng, G., 2022. Increase in rainfall intensity promotes soil nematode diversity but offset by nitrogen addition in a temperate grassland. Sci. Total Environ. 825, 154039. https://doi.org/10.1016/j.scitotenv.2022.154039

Del Grosso, S., Parton, W., Stohlgren, T., Zheng, D., Bachelet, D., Prince, S., Hibbard, K., Olson, R., 2008. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89, 2117-2126. https://doi.org/10.1890/07-0850.1

De Ruiter, P.C., Moore, J.C., Zwart, K.B., Bouwman, L.A., Hassink, J., Bloem, J., De Vos, J.A., Marinissen, J.C.Y., Didden, W., Lebbink, G., Brussaard, L., 1993. Simulation of nitrogen mineralization in the below-ground food webs of two winter wheat fields. J. Appl. Ecol. 30, 95-106. https://doi.org/10.2307/2404274

de Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Bracht Jørgensen, H., Brady, M.V., Christensen, S., de Ruiter, P.C., d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., van der Putten, W.H., Wolters, V., Bardgett, R.D., 2013. Soil food web properties explain ecosystem services across European land use systems. Proc. Natl. Acad. Sci. USA 110, 14296-14301. https://doi.org/10.1073/pnas.1305198110

du Preez, G.C., Daneel, M.S., Wepener, V., Fourie, H., 2018. Beneficial nematodes as bioindicators of ecosystem health in irrigated soils. Appl. Soil Ecol. 132, 155-168. https://doi.org/10.1016/j.apsoil.2018.08.008

Egger, M., Smith, G.D., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by a simple, graphical test. BMJ 315, 629-634. https://doi.org/10.1136/bmj.315.7109.629

Eisenhauer, N., Cesarz, S., Koller, R., Worm, K., Reich, P.B., 2012. Global change belowground: impacts of elevated CO_2, nitrogen, and summer drought on soil food webs and biodiversity. Glob. Change Biol. 18, 435-447. https://doi.org/10.1111/j.1365-2486.2011.02555.x

Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S.E., Meyer, R.J., Worm, K., Reich, P.B., 2013. Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. Proc. Natl. Acad. Sci. USA 110, 6889-6894. https://doi.org/10.1073/pnas.1217382110

Eisenhauer, N., Guerra, C.A., 2019. Global maps of soil-dwelling nematode worms. Nature 572, 187-188. https://doi.org/10.1038/d41586-019-02197-0

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802-813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Feng, H., Guo, J., Peng, C., Kneeshaw, D., Roberge, G., Pan, C., Ma, X., Zhou, D., Wang, W., 2023. Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: A global meta-analysis. Glob. Change Biol. 29, 3970-3989. https://doi.org/10.1111/gcb.16731

Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Appl. Soil Ecol. 23, 93-110. https://doi.org/10.1016/S0929-1393(03)00044-1

Ferris, H., 2010. Form and function: Metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46, 97-104. https://doi.org/10.1016/j.ejsobi.2010.01.003

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13-29. https://doi.org/10.1016/S0929-1393(01)00152-4

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302-4315. https://doi.org/10.1002/joc.5086

Gallego-Zamorano, J., de Jonge, M.M.J., Runge, K., Huls, S.H., Wang, J., Huijbregts, M.A.J., Schipper, A.M., 2023. Context-dependent responses of terrestrial invertebrates to anthropogenic nitrogen enrichment: A meta-analysis. Glob. Change Biol. 29, 4161-4173. https://doi.org/10.1111/gcb.16717

Graco-Roza, C., Aarnio, S., Abrego, N., Acosta, A.T.R., Alahuhta, J., Altman, J., Angiolini, C., Aroviita, J., Attorre, F., Baastrup-Spohr, L., Barrera-Alba, J.J., Belmaker, J., Biurrun, I., Bonari, G., Bruelheide, H., Burrascano, S., Carboni, M., Cardoso, P., Carvalho, J.C., ... Soininen, J., 2022. Distance decay 2.0 – A global synthesis of taxonomic and functional turnover in ecological communities. Global Ecol. Biogeogr. 31, 1399-1421. https://doi.org/10.1111/geb.13513

Hu, J., Kong, M., Francoys, A., Yarahmadi, F., Mendoza, O., Hassi, U., Gebremikael, M.T., Wesemael, W., Sleutel, S., De Neve, S., 2024a. Increased N_2O emissions by the soil nematode community cannot be fully explained by enhanced mineral N availability. Soil Biol. Biochem. 191, 109314. https://doi.org/10.1016/j.soilbio.2024.109314

Hu, Y., Deng, Q., Kätterer, T., Olesen, J.E., Ying, S.C., Ochoa-Hueso, R., Mueller, C.W., Weintraub, M.N., Chen, J., 2024b. Depth-dependent responses of soil organic carbon under nitrogen deposition. Glob. Change Biol. 30, e17247. https://doi.org/10.1111/gcb.17247

Huang, J., Chen, J., Huang, T., Li, G., Wang, Z., Zhao, S., 2024. Soil nematode biodiversity mediates the impact of altered precipitation on dryland agroecosystem multifunctionality in the loess tableland area of China. Agric. Ecosyst. Environ. 376, 109221. https://doi.org/10.1016/j.agee.2024.109221

Hou, W., Kuzyakov, Y., Qi, Y., Liu, X., Zhang, H., Zhou, S., 2023. Functional traits of soil nematodes define their response to nitrogen fertilization. Funct. Ecol. 37, 1197-1210. https://doi.org/10.1111/1365-2435.14293

Jiang, C., Sun, B., Li, H., Jiang, Y., 2013a. Determinants for seasonal change of nematode community composition under long-term application of organic manure in an acid soil in subtropical China. Eur. J. Soil Biol. 55, 91-99. https://doi.org/10.1016/j.ejsobi.2012.11.003

Jiang, Y., Qian, H., Wang, X., Chen, L., Liu, M., Li, H., Sun, B., 2018. Nematodes and microbial community affect the sizes and turnover rates of organic carbon pools in soil aggregates. Soil Biol. Biochem. 119, 22-31. https://doi.org/10.1016/j.soilbio.2018.01.001

Jiang, Y., Sun, B., Jin, C., Wang, F., 2013b. Soil aggregate stratification of nematodes and microbial communities affects the metabolic quotient in an acid soil. Soil Biol. Biochem. 60, 1-9. https://doi.org/10.1016/j.soilbio.2013.01.006

Jones, F.G.W., 1975. The soil as an environment for plant parasitic nematodes. Ann. Appl. Biol. 79, 113-139. https://doi.org/10.1111/j.1744-7348.1975.tb01527.x

Kane, J.L., Kotcon, J.B., Freedman, Z.B., Morrissey, E.M., 2022. Fungivorous nematodes drive microbial diversity and carbon cycling in soil. Ecology 104, e3844. https://doi.org/10.1002/ecy.3844

Keith, A.M., Brooker, R.W., Osler, G.H., Chapman, S.J., Burslem, D.F., Van Der Wal, R., 2009. Strong impacts of belowground tree inputs on soil nematode trophic composition. Soil Biol. Biochem.

41(6), 1060-1065. https://doi.org/10.1016/j.soilbio.2009.02.009

Kern, E.M.A., Kim, T., Park, J.K., 2020. The mitochondrial genome in nematode phylogenetics. Front. Ecol. Evol. 8, 250. https://doi.org/10.3389/fevo.2020.00250

Kuhn, M., 2008. Building predictive models in R using the caret package. J. Stat. Softw. 28, 1-26. https://doi.org/10.18637/jss.v028.i05

Lajeunesse, M.J., 2011. On the meta-analysis of response ratios for studies with correlated and multi-group designs. Ecology 92, 2049-2055. https://doi.org/10.1890/11-0423.1

Lajeunesse, M.J., 2015. Bias and correction for the log response ratio in ecological meta-analysis. Ecology 96, 2056-2063. https://doi.org/10.1890/14-2402.1

Lefcheck, J.S., Freckleton, R., 2015. piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573-579. https://doi.org/10.1111/2041-210X.12512

Li, B., Li, G., Kronzucker, H. J., Baluška, F., Shi, W., 2014. Ammonium stress in Arabidopsis: signaling, genetic loci, and physiological targets. Trends Plant Sci. 19(2), 107-114. https://doi.org/10.1016/j.tplants.2013.09.004

Li, C., Wang, X., Chen, B., Wang, L., Xie, Z., Wang, J., Yang, Z., 2023. Fertilization restructures nematode assemblages by modifying soil pH in croplands of Northeast China. Front. Environ. Sci. 11, 1207379. https://doi.org/10.3389/fenvs.2023.1207379

Li, D., Chen, D., Hou, C., Chen, H., Zhou, Q., Wu, J., 2025. Soil microfauna mediate multifunctionality under multilevel warming in a primary forest. J. Anim. Ecol. 94(1), 58-68. https://doi.org/10.1111/1365-2656.14210

Lie, Z., Huang, W., Liu, X., Zhou, G., Yan, J., Li, Y., Huang, C., Wu, T., Fang, X., Zhao, M., Liu, S., Chu, G., Kadowaki, K., Pan, X., Liu, J., 2020. Warming leads to more closed nitrogen cycling in nitrogen-rich tropical forests. Glob. Change Biol. 27, 664-674. https://doi.org/10.1111/gcb.15432

Lin, B.J., Cheng, J., Duan, H.X., Liu, W.X., Dang, Y.P., Zhao, X., Zhang, H.L., 2024. Optimizing straw and nitrogen fertilizer resources for low-carbon sustainable agriculture. Resour. Conserv. Recycl. 209, 107743. https://doi.org/10.1016/j.resconrec.2024.107743

Liu, T., Chen, X., Hu, F., Ran, W., Shen, Q., Li, H., Whalen, J.K., 2016. Carbon-rich organic fertilizers to increase soil biodiversity: Evidence from a meta-analysis of nematode communities. Agric. Ecosyst. Environ. 232, 199-207. https://doi.org/10.1016/j.agee.2016.07.015

Lucas, R.W., Klaminder, J., Futter, M.N., Bishop, K.H., Egnell, G., Laudon, H., Högberg, P., 2011. A meta-analysis of the effects of nitrogen additions on base cations: Implications for plants, soils, and streams. For. Ecol. Manag. 262, 95-104. https://doi.org/10.1016/j.foreco.2011.03.018

Ma, B., Sheng, X., Zhou, J., Nielsen, U.N., Wang, X., Ma, M., 2024. Phosphorus addition ameliorates soil micro-food web simplification due to nitrogen enrichment but does not restore nematode community composition. Soil Biol. Biochem. 195, 109447. https://doi.org/10.1016/j.soilbio.2024.109447

Malik, A.A., Martiny, J.B.H., Brodie, E.L., et al., 2020. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. ISME J. 14(1), 1-9. https://doi.org/10.1038/s41396-019-0510-0

Martinez, L., Wu, S., Baur, L., Patton, M.T., Owen-Smith, P., Collins, S.L., Rudgers, J.A., 2023. Soil nematode assemblages respond to interacting environmental changes. Oecologia 202, 481-495. https://doi.org/10.1007/s00442-023-05412-y

Mhlanga, B., Ercoli, L., Piazza, G., Thierfelder, C., Pellegrino, E., 2022. Occurrence and diversity of arbuscular mycorrhizal fungi colonising off-season and in-season weeds and their relationship with maize yield under conservation agriculture. Biol. Fertil. Soils 58, 917-935. https://doi.org/10.1007/s00374-022-01678-1

Mueller, K.E., Blumenthal, D.M., Carrillo, Y., Cesarz, S., Ciobanu, M., Hines, J., Pabst, S., Pendall, E., de Tomasel, C.M., Wall, D.H., Eisenhauer, N., 2016. Elevated CO_2 and warming shift the functional composition of soil nematode communities in a semiarid grassland. Soil Biol. Biochem. 103, 46-51. https://doi.org/10.1016/j.soilbio.2016.08.005

Nakagawa, S., Santos, E.S.A., 2012. Methodological issues and advances in biological meta-analysis. Evol. Ecol. 26, 1253-1274. https://doi.org/10.1007/s10682-012-9555-5

Neher, D. A., 2010. Ecology of plant and free-living nematodes in natural and agricultural soil. Annu. Rev. Phytopathol. 48(1), 394-414. https://doi.org/10.1146/annurev-phyto-073009-114439

Niu, S., Wang, S., Wang, J., Xia, J., Yu, G., 2020. Integrative ecology in the era of big data-From observation to prediction. Sci. China Earth Sci. 63, 1429-1442. https://doi.org/10.1007/s11430-020-9664-6

Paroshy, N.J., Doraisami, M., Kish, R., Martin, A.R., 2021. Carbon concentration in the world's trees across climatic gradients. New Phytol. 232, 123-133. https://doi.org/10.1111/nph.17587

Phillips, H.R.P., Cameron, E.K., Eisenhauer, N., Burton, V.J., Ferlian, O., Jin, Y., Kanabar, S., Malladi, S., Murphy, R.E., Peter, A., Petrocelli, I., Ristok, C., Tyndall, K., van der Putten, M., Beaumelle, L., 2024. Global changes and their environmental stressors have a significant impact on soil biodiversity - a meta-analysis. iScience 20, 110540. https://doi.org/10.1016/j.isci.2024.110540

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Authors, E., Heisterkamp, S., Van Willigen, B., 2018. nlme: Linear and nonlinear mixed effects models. Version. R package version 3.1-92. https://cran.r-project.org/web/packages/nlme/nlme.pdf

Poggio, L., de Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. Soil 7, 217-240. https://doi.org/10.5194/soil-7-217-2021

Puissant, J., Villenave, C., Chauvin, C., Plassard, C., Blanchart, E., Trap, J., 2021. Quantification of the global impact of agricultural practices on soil nematodes: A meta-analysis. Soil Biol. Biochem. 161, 108383. https://doi.org/10.1016/j.soilbio.2021.108383

Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. J. Ecol. 102(2), 275-301. https://doi.org/10.1111/1365-2745.12211

Rosenberg, M.S., 2005. The file-drawer problem revisited: A general weighted method for calculating fail-safe numbers in meta-analysis. Evolution 59, 464-468. https://doi.org/10.1111/j.0014-3820.2005.tb01004.x

Schloter, M., Dilly, O., Munch, J.C., 2003. Indicators for evaluating soil quality. Agric. Ecosyst. Environ. 98, 255-262. https://doi.org/10.1016/S0167-8809(03)00085-9

Shaw, E.A., Boot, C.M., Moore, J.C., Wall, D.H., Baron, J.S., 2019. Long-term nitrogen addition shifts the soil nematode community to bacterivore-dominated and reduces its ecological maturity in a subalpine forest. Soil Biol. Biochem. 130, 177-184. https://doi.org/10.1016/j.soilbio.2018.12.007

Shipley, B., 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94, 560-564. https://doi.org/10.1890/12-0976.1

Song, M., Li, X., Jing. S., Lei, L., Wang, J., Wan, S., 2016. Responses of soil nematodes to water and nitrogen additions in an old-field grassland. Appl. Soil Ecol. 102, 53-60. https://doi.org/10.1016/j.apsoil.2016.02.011

Sun, X., Zhang, X., Zhang, S., Dai, G., Han, S., Liang, W., 2013. Soil nematode responses to increases in nitrogen deposition and precipitation in a temperate forest. PLoS ONE 8(12), e82468.

https://doi.org/10.1371/journal.pone.0082468

Tenuta, M., Ferris, H., 2004. Sensitivity of nematode life-history groups to ions and osmotic tensions of nitrogenous solutions. J. Nematol. 36, 85-94.

Tian, D., Niu, S., 2015. A global analysis of soil acidification caused by nitrogen addition. Environ. Res. Lett. 10, 024019. https://doi.org/10.1088/1748-9326/10/2/024019

Tian, Y., Wang, X., Guo, K., Islam, M. N., Liu, X., Liang, W., Zhang, X., 2024. Stover management affects soil food webs and regulates the decomposition pathway in a maize field. Agric. Ecosyst. Environ. 376, 109229. https://doi.org/10.1016/j.agee.2024.109229

Tibbett, M., Gil-Martínez, M., Fraser, T., Green, I.D., Duddigan, S., De Oliveira, V.H., Raulund-Rasmussen, K., Sizmur, T., Diaz, A., 2019. Long-term acidification of pH neutral grasslands affects soil biodiversity, fertility and function in a heathland restoration. Catena 180, 401-415. https://doi.org/10.1016/j.catena.2019.03.013

Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. Ecol. Lett. 11, 1111-1120. https://doi.org/10.1111/j.1461-0248.2008.01230.x

Ugarte, C.M., Zaborski, E.R., Wander, M.M., 2013. Nematode indicators as integrative measures of soil condition in organic cropping systems. Soil Biol. Biochem. 64, 103-113. https://doi.org/10.1016/j.soilbio.2013.03.035

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., ... Crowther, T. W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194-198. https://doi.org/10.1038/s41586-019-1418-6

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. J. Stat. softw. 36, 1-48. https://doi.org/10.18637/jss.v036.i03

Wang, H.L., Liu, G.C., Huang, B.B., Wang, X.C., Xing, Y.J., Wang, Q.G., 2021. Long-term nitrogen addition and precipitation reduction decrease soil nematode community diversity in a temperate forest. Appl. Soil Ecol. 162, 103895. https://doi.org/10.1016/j.apsoil.2021.103895

Wei, C., Zheng, H., Li, Q., Lü, X., Yu, Q., Zhang, H., Chen, Q., He, N., Kardol, P., Liang, W., Han, X., 2012. Nitrogen addition regulates soil nematode community composition through ammonium suppression. PLoS ONE 7, e43384. https://doi.org/10.1371/journal.pone.0043384

Xing, A., Du, E., Shen, H., Xu, L., de Vries, W., Zhao, M., Liu, X., Fang, J., 2022a. Nonlinear responses of ecosystem carbon fluxes to nitrogen deposition in an old-growth boreal forest. Ecol. Lett. 25(1), 77-88. https://doi.org/10.1111/ele.13906

Xing, W., Lu, X., Niu, S., Chen, D., Wang, J., Liu, Y., Wang, B., Zhang, S., Li, Z., Yao, X., Yu, Q., Tian, D., 2022b. Global patterns and drivers of soil nematodes in response to nitrogen enrichment. Catena 213, 106235. https://doi.org/10.1016/j.catena.2022.106235

Xiong, D., Wei, C.Z., Wubs, E.R.J., et al., 2020. Nonlinear responses of soil nematode community composition to increasing aridity. Global Ecol. Biogeogr. 29(1), 117-126. https://doi.org/10.1111/geb.13013

Xiong, D., Wei, C., Wang, X., Lü, X., Fang, S., Li, Y., Wang, X., Liang, W., Han, X., Bezemer, T. M., Li, Q., 2021. Spatial patterns and ecological drivers of soil nematode β-diversity in natural grasslands vary among vegetation types and trophic position. J. Anim. Ecol. 90, 1367-1378. https://doi.org/10.1111/1365-2656.13461

Xu, H., Qu, Q., Li, G., Liu, G., Geissen, V., Ritsema, C.J., Xue, S., 2022. Impact of nitrogen addition on plant-soil-enzyme C-N-P stoichiometry and microbial nutrient limitation. Soil Biol. Biochem. 170, 108714. https://doi.org/10.1016/j.soilbio.2022.108714

Yan, D., Yan, D., Song, X., Yu, Z., Peng, D., Ting, X., Weng, B., 2018. Community structure of soil nematodes under different drought conditions. Geoderma 325, 110-116. https://doi.org/10.1016/j.geoderma.2018.03.028

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37, 199-210. https://doi.org/10.1007/s00374-003-0586-5

Zhang, C., Wright, I. J., Nielsen, U. N., Geisen, S., Liu, M., 2024. Linking nematodes and ecosystem function: a trait-based framework. Trends Ecol. Evol. 39, 644-653. https://doi.org/10.1016/j.tree.2024.02.002

Zhang, T., Chen, H. Y. H., Ruan, H., 2018. Global negative effects of nitrogen deposition on soil microbes. ISME J. 12, 1817-1825. https://doi.org/10.1038/s41396-018-0096-y

Zhou, J., Wu, J., Huang, J., Sheng, X., Dou, X., Lu, M., 2022. A synthesis of soil nematode responses to global change factors. Soil Biol. Biochem. 165, 108538. https://doi.org/10.1016/j.soilbio.2021.108538

Zhou, Q., Xiang, Y., Li, D., Luo, X., Wu, J., 2021. Global patterns and controls of soil nematode responses to nitrogen enrichment: A meta-analysis. Soil Biol. Biochem. 163, 108433. https://doi.org/10.1016/j.soilbio.2021.108433

Figure legends:

Fig. 1. The responses of soil nematodes to N enrichment. The overall mean effect size and responses of the abundance of nematodes, diversity and ecological indices to N enrichment, and these response as affected by ecosystem type (cropland, forest, and grassland) and type of N fertilizer (NH_4NO_3, urea, organic fertilizers and others). The circles and error bars show the mean estimate along with the 95% confidence interval (CI). If the 95% CIs does not overlap with zero, the N-enrichment effect was deemed statistically significant. The numbers on the right side of each panel denote the number of effect sizes and the respective number of studies included in this meta-study. Effect sizes are expressed as corrected response ratios ($lnRR^{\Delta}$).

Fig. 2. Multilevel meta-regression models examining the effects of environmental moderators of N enrichment effects, including MAT **(a)**, aridity index **(b)**, background soil pH **(c)**, and experiment duration **(d)** on the relationships between corrected response ratio ($lnRR^{\Delta}$) of nematode parameters to N enrichment rate. Continuous variables are represented as quantile values of 5%, 25%, 50%, 75%, and 95% for each moderator. The solid line represents the model estimate of the relationship between the $lnRR^{\Delta}$ and N enrichment rate at a specific quantile for each moderator, and shaded areas represent 95% confidence intervals. Q_M and P values indicate the interaction effect, where the slope changes with varying values of the tested moderator, or the intercept effect where the slope does not change but the intercept changes with varying values of the tested moderator. MAT, mean annual temperature; Aridity index,

the ratio of precipitation over potential evapotranspiration; pH, soil pH; Durtion, experiment duration.

Fig. 3. Model-averaged importance of the predictors of the corrected response ratio (*$lnRR^{\Delta}$*) of N enrichment on the nematode abundances **(a)**, diversity and ecological indices **(b)**. The relative importance value is based on the sum of the Akaike weights derived from the model selection using corrected Akaike's Information Criteria. The cutoff is defined at 0.8 to distinguish essential predictors from nonessential ones.

Fig. 4. Piecewise structural equation model (SEM) depicting the influence of the N enrichment rates (Rate), experimental duration (Duration), mean annual temperature (MAT), aridity index (AI), corrected response ratios ($lnRR^{\Delta}$) of environment factors (SOC, TN, NH_4^+, NO_3^- and pH) on the $lnRR^{\Delta}$ of nematodes abundances **(a-e)**, diversity **(f)**, and ecological indices **(g-i)**. Arrows indicate the directionality of the relationship, and the numbers beside the arrows are standardized coefficients. The arrow (path) thickness is proportional to the standardized path coefficient, with solid purple and green arrows representing positive and negative effects, respectively. To improve overall readability, the corrected response ratios ($lnRR^{\Delta}$) of SOC and TN, or NH_4^+ and NO_3^- are plotted within a box rather than constructing latent variables, and ①②③④ denote the paths where a certain variable directs towards SOC, TN, NH_4^+, NO_3^-, or where these four variables direct towards other variables, respectively. SOC, TN, NH_4^+, NO_3^-, and pH represent the $lnRR^{\Delta}$ of soil organic carbon, total nitrogen, ammonium,

nitrate, and pH, respectively.

Fig. 5. Spatial patterns of soil nematode abundances in response to N deposition in the Northern Hemisphere. (a-e) The spatial patterns of effect sizes ($lnRR^{\Delta}$) of soil nematode abundances (total nematode abundance, plant-feeding nematodes, fungal-feeding nematodes, bacterial-feeding nematodes, and omnivorous-predatory nematodes; from the top to bottom of the figure) and their latitudinal gradients. To minimize uncertainties arising from geographic bias in extrapolation prediction, we excluded regions with sparse sample distributions, including the entire Southern Hemisphere, major desert areas, and Greenland. The key regions are marked with black boxes. The shaded area in represents 1 standard deviation. The results of 100 iterations of bootstrap resampling and uncertainties of spatial prediction are shown in Figs. S13 and S14, respectively. **(f-j)** The relationships between global soil nematode abundances (individuals per 100 g dry soil; van den Hoogen et al., 2019) and global N deposition rate (kg N ha^{-1} yr^{-1}; Ackerman et al., 2019) from previously published global raster maps. The red, black, and blue solid lines indicate the results of linear, quadratic, and generalized additive models, respectively. Globally, soil nematode abundances decreased with increasing N deposition rate.