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Global nitrogen enrichment impacts plant diversity more than soil bacterial and fungal diversity: a meta-analysis

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Abstract

Anthropogenic nitrogen enrichment has significant effects on plant and soil biodiversity across local to global scales, yet how the nitrogen-induced changes in plant diversity differ from those in soil organisms across multiple ecosystems and climatic conditions remains virtually unknown. By synthesizing plant and soil studies globally (3,816 paired observations from 458 articles), we demonstrate that N enrichment has stronger negative effects on plant diversity but surprisingly modest to negligible effects on soil bacterial and fungal diversity. On average, N enrichment results in 8.3% and 10.3% reductions in species richness and Shannon index for plants. In contrast, it leads to 1.9% and 0.2% reductions for soil bacteria and < 0.4% changes for soil fungi, respectively. The N-induced soil acidification modulates soil biodiversity change and, in conjunction with aboveground biomass, regulates plant biodiversity change. Our findings provide a perspective on the differential impacts of global N enrichment on above- and below-ground biodiversity, highlighting the need for integrated biodiversity conservation strategies.

Introduction

Biodiversity is fundamental for the functioning, resilience, and productivity of ecosystems and for the health and stability of the biosphere[1-5]. Diverse plant communities provide various ecosystem services, from carbon sequestration, climate change mitigation and cultural services to support of a wider array of species, including soil biota, when compared with low-plant diversity ecosystems[6-8]. Similarly, diverse soil communities plays a critical role in key ecological processes such as decomposition, nutrient cycling, carbon storage, and disease regulation, which in turn enhance plant diversity and productivity[2,4,9,10]. The intricate interplay between plant and soil communities is essential for maintaining ecosystem functions and services, as well as for responding to climate change and other anthropogenic pressures[11-14]. Losses in either plant or soil biodiversity can trigger cascading ecosystem dysfunction, with detrimental consequences for both natural systems and human well-being[15-17]. While changes in plant diversity often influence soil

biodiversity and composition[11,13,18], plant and soil communities can exhibit divergent responses to anthropogenic stressors[5], mainly due to their fundamental differences in life-history traits, environmental sensitivity, and resource dependence[19,20]. Therefore, we need to better understand the combined and interactive nature of plant and soil biodiversity responses to global change across multiple ecosystems and climatic conditions.

Anthropogenic nitrogen (N) enrichment (including atmospheric N deposition, N fertilization or N addition), a pervasive component of global change, is projected to continue[21], which may increasingly harm plant and soil biodiversity[22-27]. Plant diversity is often negatively affected by N enrichment with non-linear patterns[28], mainly due to the increased competition for light and other resources[26,29,30], soil acidification[25,31], and reduced niche dimensionality[32,33]. The magnitude of these effects is further modulated by environmental conditions and the responsiveness of primary production[34,35]. Nitrogen affects soil biodiversity primarily through changing soil pH and nutrients availability, which directly alter competition advantages among taxa and their niche convergence[36-38]. Given larger variations in taxonomic or functional groups of soil organisms compared to plants[20,39], soil microbial communities have exhibited variable responses to N enrichment, ranging from positive to neutral to negative, depending on environmental context[27,40,41]. Moreover, the effects of N enrichment and the feedbacks between plants and soils are influenced by climatic and edaphic conditions[25,34,35,42-45]. The lack of holistic integrated understanding of these context-dependent responses (our goal herein) strongly limits our capacity to predict how terrestrial ecosystems might respond to ongoing global N enrichment.

Previous studies have examined the effects of global change factors (including N enrichment) on plant richness and soil biodiversity separately (Supplementary Table 1). However, they have not addressed two critical questions: (i) Do plant and soil biodiversity respond divergently to N enrichment? and (ii) How do these responses vary across different climates and biomes? These knowledge gaps hinder our ability to contrast the effects of N on these interconnected communities and to understand how plant communities mediate N effects on soil communities, and vice versa.

Despite the close association between plant and soil biodiversity, plant diversity is often more directly influenced by aboveground resource competition (e.g., light, space) and soil acidification[25,26,29-31], whereas soil biodiversity is shaped by belowground conditions such as pH, nutrient stoichiometry, and organic matter inputs[9,46,47], and usually depends on the taxonomic or functional groups and environmental context[27,40,41]. We therefore hypothesize that plant diversity may respond more consistently and strongly to N enrichment, while soil biodiversity show weaker or more context-dependent responses. Herein, we perform a global synthesis using 3,816 paired observations from 458 N enrichment studies across 366 sites in 31 countries. Our global dataset contain control and N enrichment treatments covering a wide range of N enrichment rates at sites with contrasting mean annual temperature and precipitation (i.e., binned into three major climate zones for certain purposes: tropical, temperate and boreal), soil pH and ecosystem types (i.e., croplands, grasslands and forests) (Supplementary Fig. 1 and Table 2). We first conduct a meta-analysis to evaluate the effects of N on plant and soil biodiversity, testing the climatic and biome context dependency. We report richness (e.g., the number of species) and Shannon index as metrics of plant and soil biodiversity, which jointly capture the number of taxa and their relative abundance distribution. However, due to limited data availability, we include only the Shannon index for soil nematodes. We focus on standardized effect size expressed at a common rate (25 kg N ha^{-1} $year^{-1}$) and duration (10 years) of N treatment to minimize the bias induced by variations in these two factors (see Methods). We use model selection and regression analyses, followed by structural equation modelling, to identify the key factors modulating N effects. We find that N enrichment impacts plant diversity more than soil bacterial and fungal diversity, underscoring the need for integrated approaches to mitigate the impacts of N enrichment on both above- and below-ground biodiversity.

Result and Discussion

Effects of N enrichment on soil properties

Nitrogen enrichment increased the concentrations of soil total and available N, as well as organic carbon (Supplementary Fig. 2), but decreased soil pH (Supplementary Fig. 3), indicating N-induced soil acidification. Soil N and organic carbon increases were greater in grasslands and forests than in croplands. Among the three climates, organic carbon and ammonium N increases were greater in boreal climates. In contrast, soil nitrate N increase was greater in tropical climates compared with other climates. Overall, the increase in total N was comparable among the three climates. The N enrichment-induced soil acidification was significantly greater in grasslands and croplands than in forests, and it was also notably higher in temperate climates compared to boreal and tropical climates. This pattern primarily stems from the fact that these ecosystems and climate regions generally have higher background soil pH levels (Supplementary Fig. 3), while the reduction in soil pH due to N enrichment is significantly negatively correlated with background soil pH (Supplementary Fig. 3). Furthermore, ammonium N has a more pronounced effect on soil pH than other forms of N (Supplementary Fig. 3).

Effects of nitrogen enrichment on plant diversity

Nitrogen enrichment had relatively strong negative effects on plant biodiversity (Fig. 1), in agreement with previous studies[22,23,25,26,45]. The negative effect of N (at the common rate of 25 kg ha^{-1} $year^{-1}$ for 10 years) for plant species richness averaged -8.3% over forests and grasslands, being similar for these two ecosystems (mean effect size (E_{ComN}): -10.3% and -8.1%, 95% confidence interval (CI): -13.9 to -6.6% and -8.8 to -7.4%, all $P < 0.05$). Shannon index showed similar trends between forests and grasslands (E_{ComN}: -3.6% and -2.5%, CI: -12.4 to 6.2 and -4.2 to -0.8%).

Among the three main climate zones, the negative effect of N on plant species richness was significantly greater in boreal (including arctic) climates (E_{ComN}: -19.5%, CI: -25.4 to -13.2%, $P < 0.05$), followed by temperate (E_{ComN}: -8.3%, CI: -9.0 to -7.5%, $P < 0.05$) and tropical (including subtropical) climates (E_{ComN}: -6.3%, CI: -8.4 to -4.3%, $P < 0.05$). Similarly, plant Shannon index also showed a significant negative response to N enrichment in boreal climates (E_{ComN}: -16.3%,

CI: -23.0 to -9.0%, $P < 0.05$) but not in other climates (Fig. 1). This more negative effect in boreal climates may arise from intensified interspecific competition induced by N enrichment, as boreal regions receive lower N inputs (Supplementary Fig. 4) and N limitation is common in cold high-latitude ecosystems[48,49]. Therefore, exogenous N inputs may stimulate the growth of certain fast-growing species, enabling them to outcompete others for limited resources, thereby reducing overall diversity. This explanation is supported by the significantly greater N enrichment-induced increase in plant aboveground biomass in boreal compared to other climates (Supplementary Fig. 5a). This increase was negatively correlated with declines in plant diversity (Supplementary Fig. 5b-c), as an increase in aboveground biomass typically enhances competition for light[30]. Our findings underscore the complex and context-dependent effects of N enrichment on plant diversity across ecosystems and climate zones.

Effects of nitrogen enrichment on soil biodiversity

When averaged across ecosystems and climates, N enrichment significantly but very modestly reduced the diversity of soil bacteria (E_{ComN}: -1.9% and -0.2%, CI: -3.3 to -0.5% and -0.2 to -0.1%, for richness and Shannon index, respectively, all $P < 0.05$) and soil nematodes (E_{ComN}: -2.2%, CI: -3.0 to -1.5% for Shannon index, $P < 0.05$) but not of total soil fungi (E_{ComN}: +0.2% and +0.4%, CI: -0.4 to 0.8% and 0 to 0.7%) (Fig. 1). The negative effects on soil bacteria and nematodes are associated with increased soil acidification and elevated soil N concentration[50,51] (Fig. 2 and Supplementary Figs. 2, 3, 6), which disrupt bacterial energy metabolism by impairing proton gradients[36,37] and reduced the ability of nematodes to regulate osmotic pressure[52]. These processes modestly enhance the competitive advantage of well-adapted taxa in acidified soils, resulting in ecological niche convergence and thereby decreased diversity[36-38]. Conversely, fungal cell membranes exhibit greater tolerance to low pH conditions, allowing fungi to thrive[45] and occupy niches that are less suitable for bacteria[37,52]. Furthermore, the symbiotic relationships between fungi and plants may also provide a buffering effect against soil acidity[53]. The lack of N

enrichment effects on total fungi may also be related to contrasting N effects on different fungal guilds[54-56].

Among the three ecosystem types, N enrichment reduced bacterial and nematode diversity in grasslands and/or croplands (Fig. 1). This trend likely stems from greater reductions in soil pH in these two ecosystems (Supplementary Fig. 3), inasmuch as the biodiversity of both bacteria and nematodes is strongly affected by soil pH (Fig. 2). In forests, N enrichment significantly increased the overall fungal Shannon index (E_{ComN}: +1.6%, CI: +0.6 to +2.7%, $P < 0.05$). We ascribe this increase to elevated soil phosphorous availability, which positively correlates with fungal diversity[57-59]. Nitrogen enrichment usually increases phosphorus availability by increasing phosphatase activities[60,61] and promoting the dissolution of immobile inorganic phosphorous to more available forms[62]. This explanation is supported by meta-analytical evidence showing that N enrichment results in consistently increase of soil phosphatase activities in forests[63].

Nitrogen enrichment had divergent effects on soil biodiversity in different climates. In temperate regions, N enrichment reduced bacterial richness (E_{ComN}: -1.7%, CI: -3.2 to -0.2%, $P < 0.05$) and Shannon index (E_{ComN}: -0.2%, CI: -0.5 to 0%, $P > 0.05$) and nematode Shannon index (E_{ComN}: -2.5%, CI: -3.3 to -1.8%, $P < 0.05$) (Fig. 1). This is likely related to the stronger acidification in this climate zone compared to the other climates (Supplementary Fig. 3), as the biodiversity of both bacteria and nematodes is strongly influenced by soil pH reduction (Fig. 2). In contrast, N enrichment significantly increased fungal richness (E_{ComN}: +5.9%, CI: +2.0 to +9.9%, $P < 0.05$) and Shannon index (E_{ComN}: +4.7%, CI: +2.5 to +6.9%, $P < 0.05$) in boreal region (Fig. 1), likely due to the increased plant productivity (Supplementary Fig. 5) and soil organic carbon (Supplementary Fig. 2) in this resource-limited region[40,64]. Fungi, which are highly sensitive to resource availability[50], may benefit from these changes. This process, however, may not apply to temperate and tropical regions, where fungi have adapted to a relatively high N environment.

More substantial nitrogen effects on plant diversity than on soil bacterial and fungal diversity

To compare the effects of N enrichment on plants versus soil biota, we conducted Z-tests across the entire global dataset and within specific ecosystem types or climate zones (Table 1). Across the global dataset, N enrichment-induced changes in the Shannon index and species richness were significantly greater in plants than in soil bacteria ($Z = 2.9$ and 8.1, $P < 0.01$) and fungi ($Z = 3.49$ and 17.59, $P < 0.001$). However, the change in Shannon index for plants (-2.6%) was comparable to that for soil nematodes (-2.2%) ($Z = 0.4$, $P = 0.7$). Within ecosystem types or climate zones, 15 out of 20 comparisons between plants and soil bacteria/fungi were significant ($P < 0.05$) or marginally significant ($P < 0.10$), and these all showed greater declines for plants.

To enable a more direct comparison, we extracted independent studies from our global dataset that included both plant and soil biota (bacteria, fungi, or nematodes) and performed an additional meta-analysis (Table 2). Our Z-test on this meta-analysis showed that N enrichment-induced changes in plant diversity were significantly greater than those in soil bacteria ($Z = 6.8$ and 5.4 for Shannon index and richness, $P < 0.001$) and fungi ($Z = 6.5$ and 6.9, $P < 0.001$), but were similar to those in soil nematodes ($Z = 0.4$, $P = 0.7$).

We further examined how changes in biodiversity with N enrichment rates vary between plants and soil biotas by using meta-regression. We found that plant and soil biodiversity exhibited more pronounced negative effects at higher N rates, but the decline in plant diversity was significantly steeper than that in soil biodiversity ($P < 0.01$ for the comparison between plant and any group of soil biota, Fig. 3). This indicates that plant diversity is more sensitive to elevated N enrichment rates than soil biodiversity.

These comparisons collectively demonstrate that N enrichment has more pronounced negative effect on plant biodiversity than soil bacterial or fungal biodiversity. The increase in plant aboveground biomass under N enrichment (Supplementary Fig. 5) creates shading effects that disproportionately impact plant communities, while soil biota remain relatively unaffected (Fig.

2). Soil organisms, embedded in complex food webs with diverse trophic interactions and niche differentiation[65-67], exhibit greater ability to withstand N enrichment[68,69]. In contrast, plants, as autotrophs, have less complex interactions and niche differentiation, making them more vulnerable to N-induced changes[67,70,71]. Additionally, for plant communities, N enrichment-induced shading effects result in asymmetric light competition where larger plants dominate over smaller ones[72]. Whereas, soil biota communities are less affected by light competition as their dynamics are independent on light availability[73].

Factors regulating nitrogen enrichment effects on plant and soil biodiversity

Our meta-regression analysis revealed that N enrichment-induced changes in plant diversity were negatively correlated with increases in soil N and plant biomass, but positively correlated with reductions in soil pH (Fig. 2). Similarly, changes in soil bacterial and nematode diversity were also negatively correlated with increases in soil N and positively correlated with soil pH reduction.

The results from structural equation modeling and model selection analyses identified soil mineral N (ammonium or nitrate) concentration, plant aboveground biomass, and soil pH reduction as the primary factors regulating changes in plant diversity (Figs. 4-5). Soil ammonium concentration and pH also served as key moderators for N enrichment-induced changes in bacterial diversity, with the effects of pH being greater than those of ammonium. For nematode diversity, soil pH was the sole moderating factor. Conversely, N enrichment-induced changes in fungal diversity were unaffected by these factors. Climate indirectly influenced biodiversity changes by modulating soil pH (Fig. 4).

Implications

Our meta-analysis demonstrated significant reduction in plant diversity induced by N enrichment, which would have potential cascading effects on ecosystem functioning[9].

Conservation strategies should prioritize reducing N pollution, mitigating soil acidification through liming or biochar amendments[74], and reintroducing native species that are less sensitive to N. Encouraging biological interactions that enhance nutrient cycling and retention[75] and reintroducing mammalian herbivores to suppress dominance in grasslands[76] could also help mitigate biodiversity and functional losses under climate change. Restoration projects should consider increasing plant diversity to mitigate the negative effects of N enrichment on biodiversity and improve ecosystem functioning.

Besides to implications for conservation and management, our study adds insights into how global N enrichment has affected biodiversity by demonstrating more pronounced effects on plant diversity than on soil bacterial and fungal diversity. This divergence implies reduced links between these two aspects of biodiversity under higher N environments, which may lead to the decoupling of plant-soil biodiversity. Our study highlights the critical roles of increased aboveground biomass in reducing plant diversity and soil pH decline in reducing soil biodiversity, explaining the pronounced effects of N in boreal regions for plants and temperate regions for soil organisms. Given the fundamental role of biodiversity in terrestrial ecosystems[1-5], our findings underscore the importance of increasing plant and soil communities' resilience to N enrichment to maintain ecosystem health and plant and soil biodiversity. Future research should focus on the responses of specific functional groups of plants and soil biota, particularly those involved in N cycling and ecosystem functions, to better understand N-ecosystem feedbacks.

Limitations

For most meta-analyses in ecological studies, there usually is a geographic bias due to the over-concentration of publications in some specific regions (e.g., Eastern Asia, Europe, and Northern America) and the omission of data in other regions (e.g., Southern America, Africa, Oceania)[77-79]. Consequently, the dataset primarily reflects N effects in areas with historically high N deposition, while regions with lower or more variable N inputs remain underrepresented. The

lack of data from underrepresented regions and certain subgroups (e.g., boreal region) may limit a robust assessment of N enrichment effects in those regions and/or subgroups, and hence restrict the generalizability of our findings. Such constraint hampers the ability to detect climate-driven differences across regions and to predict ecosystem responses across the full spectrum of global N regimes, underscoring the need for expanded research efforts to fill these critical geographic knowledge gaps. In our study, the average N enrichment rate (ca. 100 kg N ha^{-1} $year^{-1}$) significantly exceeds current global N deposition rate[80,81] (< 50 kg N ha^{-1} $year^{-1}$), indicating that our conclusions hold mainly for high N enrichment scenarios. Their applicability to regions where only N inputs are dominated by atmospheric deposition warrants further investigation. Additionally, modelling uncertainty should be considered when constructing global projections of a variable in response to a global change factor. However, notwithstanding these limitations, our study remains the greatest effort to comprehend changes in plant and soil biodiversity driven by N deposition at the global scale.

Methods

Data collection

We compiled a global dataset to examine N enrichment's effects on plant and soil (bacteria, fungi and nematode) diversity (Supplementary Data 1). We followed the guidelines of PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) (Supplementary Fig. 7)[82] to systematically search for peer-reviewed journal articles and theses that report the effects of N enrichment on soil properties, soil microbes, nematodes and plants in various terrestrial ecosystems, using the Web of Science (Core Collection; https://www.webofknowledge.com), Google Scholar (https://scholar.google.com), and the China National Knowledge Infrastructure (CNKI; https://www.cnki.net) to August 1st, 2023. The search strings were composed of "OR" and "AND" statements combining terms related to N enrichment experiments and diversity of plant species and soil biota, i.e. ("nitrogen fertilization", "nitrogen deposition", "nitrogen addition"

OR “nitrogen enrichment”) AND (“richness” OR “diversity”) AND (“plant” OR “soil microbial” OR “soil bacteria” OR “soil fungi” OR “soil nematode”).

We evaluated each study to determine whether it met the following criteria to ensure the quality of the data. (1) N was directly added to the ecosystems and at least one of the considered variables was measured (including plant/bacterial/fungal richness and Shannon index, nematode Shannon index). (2) N-enrichment and control plots were established under the same abiotic and biotic conditions in the field. Furthermore, laboratory incubation studies were excluded. (3) In studies involving additional global change drivers (e.g., warming, altered precipitation, phosphorus fertilization), only N-enrichment and control plots under matched field conditions were included. Plots with non-nitrogen treatments were excluded to isolate the effects of N enrichment. (4) Experiments applying herbicide, fungicide, or pesticide were retained only if treatments were consistent across both N-enrichment and control plots; otherwise they were excluded. (5) Plant diversity in croplands was not included because plant communities are highly modified and managed for agricultural purposes. (6) N treatment was applied continuously from the first application to the measurement, with duration calculated in years based on the interval between the first and final application, including repeated treatments within a year. (7) The means, standard deviation (SD) and sample sizes (n) of the variables selected were reported or could be calculated from the related results, and the standard error (SE) was converted to SD ($SD = SE \times \sqrt{n}$). (8) If multiple independent experiments conducted under different environmental conditions or ecosystem types were reported in the same publication, each experiment was considered an independent data record. (9) The type of N added, rate and duration of N enrichment were directly reported. The N enrichment rate and duration units were converted to common units of kg N ha^{-1} $year^{-1}$ and year, respectively. (10) We included only observations where soil samples were collected from the mineral soil layer, typically within the top 0-20 cm.

Metrics describing plant and soil biodiversity, climates, and soil properties

The metrics of plant diversity included plant species richness and the Shannon index. The plant species richness was investigated by the total number of species recorded in its quadrat, and the Shannon index was calculated based on this measurement. The diversity metrics of soil bacteria and fungi included richness (Chao1 and/or OTU number) and the Shannon index, and that of nematodes included the Shannon index. Soil nematodes was identified to genera based on morphological characteristics per 100 g of dry soil from each sample using a modified Baermann wet funnel technique, and the Shannon index was calculated based on this measurement. In our dataset, the microbial diversity assessments varied in sequencing depth, taxonomic resolution, and methodological approaches among independent studies. However, since all comparisons were performed between treatment and control conditions within the same study, the difference in technical variations did not affect our comparison and could be neglected in this meta-analysis.

We also collected ancillary data, including climatic variables, soil properties, ecosystem types, type of N used in the experiment, and rate and duration of N enrichment. The climatic variables used in this study included mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), and the aridity index (AI, unitless). The MAT and MAP were directly obtained from the publications, or in case they were not reported, from the database at http://www.worldclim.org/ using the location information (i.e., latitude and longitude) covering the years over which each experiment was conducted. The aridity index was extracted from the Global Aridity and Potential Evapotranspiration database at https://csidotinfo.wordpress.com/data/global-aridity-and-pet-database/. The soil properties were directly extracted from the publications. The soil properties included soil pH (1:2.5 or 1:5 soil:water (w/v), or KCl or $CaCl_2$ mixture), soil moisture, and the concentrations of soil organic carbon (dichromate oxidation or elemental analyzer), total N (Kjeldahl or elemental analyzer), nitrate and ammonium N (flow injection analysis or spectrophotometric). The indices from different analytical methods were standardized to common units to ensure comparability. The experimental protocols (i.e., rate of N enrichment, duration of

the experiment, type of N used in the experiment) were also directly extracted from the publications.

Our final dataset contained 3,816 paired observations from 458 N-enrichment studies at 366 sites in 31 countries. The dataset covered a wide range of N enrichment rates, latitude, longitude, MAP and MAT, and soil background pH (Supplementary Fig. 1 and Table 2). All the original data were extracted from the publications' text, tables, figures, and appendices. The Engauge software 4.1 obtained numeric data (http://getdata-graph-digitizer.com) when the data were graphically presented.

We grouped the data in the set by ecosystem type and climatic region to determine how the effects of N enrichment varied with ecosystem types and climatic regions. The ecosystem types were grouped into croplands, forests and grasslands. The diversity in forests was referred to understory vegetation. The climatic regions were grouped into tropical (tropical and subtropical regions), temperate, and boreal (boreal and polar regions) regions based on the 2010 map of Global Ecological Zones (https://data.apps.fao.org/).

Publication bias

We performed a series of analyses to evaluate the potential for publication bias. First, we conducted a funnel plot analysis to assess the bias against publishing negative results, and we tested the asymmetry of the funnel plot using Egger's regression test[83]. If asymmetry was detected, we further evaluated the sensitivity of our results to publication bias with the Rosenberg fail-safe number[84]. Additionally, to evaluate potential publication time-lag bias, where studies with larger or significant effects are published earlier, we included publication year as a continuous moderator in the meta-regression. This allowed us to test whether effect sizes declined over time, which could indicate inflated early estimates and assess the robustness of the overall results[85]. Finally, we assessed the robustness of our results through a leave-one-out analysis.

Our analyses revealed no evidence of publication bias regarding the effects of N enrichment on the richness and Shannon index of plants and soil bacteria, as well as on the Shannon index of soil nematodes (Supplementary Table 3 and Fig. 8; Egger's test: $P > 0.05$). However, we detected asymmetry in the funnel plot for the effects of N enrichment on the richness and Shannon index of soil fungi (Supplementary Table 3 and Fig. 8; Egger's test: $P < 0.05$). Despite this asymmetry, the Rosenberg fail-safe numbers for these two metrics were significantly larger than the threshold of 5k + 10 (Supplementary Table 3), suggesting that publication bias is unlikely to impact our findings regarding the effects of N enrichment on plant and soil biodiversity.

Our examination on publication time-lag bias did not show larger positive effect sizes in earlier studies compared to more recent studies for nearly all biodiversity indices, except for the Shannon index of soil bacteria ($P = 0.027$) (Supplementary Fig. 9). Given that we strengthen our conclusions by incorporating two metrics of diversity (i.e., richness and the Shannon index), the publication year may have had limited impact on our results. Moreover, the results from the leave-one-out analysis indicated that the effect size was not significantly altered by the removal of any single independent study (Supplementary Fig. 10), further confirming that the effects of N enrichment in our study are not driven by any single influential study. We further examined the publication bias for each climate-zone and ecosystem-type subgroup for all metrics. We found that, except for soil bacterial richness in forests and bacterial Shannon index in grasslands, 43 out of 45 examinations showed symmetric funnel plots and exceeded the 5K + 10 fail-safe threshold (Supplementary Table 4), indicating no publication bias for the vast majority of subgroups. Collectively, the outcomes of these three analyses suggest that our findings are robust against publication bias.

Meta-analysis

We quantified the response of each variable to N enrichment across the global dataset by calculating the effect size as the natural logarithm of the response ratio (*lnRR*), that is, the natural

logarithm of the ratio of the mean of the treatment groups to the mean of the control groups[86]. The *lnRR* was calculated as follows:

$$lnRR = \ln\frac{X_N}{X_{CK}} = \ln(X_N) - \ln(X_{CK}) \quad \text{(Eq. 1)}$$

where X_N and X_{CK} are the mean values of a given variable in the N-enrichment and control treatment, respectively. Soil pH uses a logarithmic scale, so N enrichment's effects on pH were calculated as the difference between the treatment and control groups ($pH_N - pH_{CK}$).

We also quantified such response within various groups of ecosystems and climates by weighting the $lnRR$ with the inverse of the variance and a random-effect model. The weighted mean response ratio ($lnRR_+$) was calculated as follows:

$$lnRR_+ = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij} lnRR}{\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij}} \quad \text{(Eq. 2)}$$

where m is the number of observations in every corresponding compared group, and n represents the number of groups.

The weighting factor (w_{ij}) of the individual observation was calculated as:

$$w_{ij} = \frac{1}{v_{ij} + c^2} \quad \text{(Eq. 3)}$$

where c^2 is the between observations variance.

The variance (v_{ij}) of individual observation was calculated as:

$$v_{ij} = \frac{S_N^2}{n_N X_N^2} + \frac{S_{CK}^2}{n_{CK} X_{CK}^2} \quad \text{(Eq. 4)}$$

where n_N and n_{CK} are the sample sizes for the N-enrichment and control treatments, respectively, and S_N and S_{CK} are the standard deviations for the N-enrichment and control treatments, respectively, of the *i*th observation.

The standard error of *lnRR* was calculated as:

$$s(lnRR_+) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij}}} \quad \text{(Eq. 5)}$$

The 95% confidence interval (*CI*) for $\ln RR$ was calculated as:

$$95\%CI = lnRR_+ \pm 1.96 s(lnRR_+) \quad \text{(Eq. 6)}$$

The weighted percent effect size for plant and soil variables induced by N enrichment in a group of ecosystems or climates was calculated as:

$$Effect\ size(\%) = (\exp(lnRR_+) - 1) \times 100\% \quad \text{(Eq. 7)}$$

We first conducted a meta-analysis using our global dataset to assess the overall effects of N enrichment on plant and soil variables and to assess how these effects vary with ecosystem types and climate regions. We conducted between-group heterogeneity tests (Q_B) to compare the effects of N enrichment on each metrics among subgroups of ecosystem types or climate regions[87], and conducted Z-test to compare the effects of N enrichment on diversity between plant and soil biota[88]. We then extracted the independent studies that include both plant and any group of soil biota (bacteria, fungi, or nematodes) from the whole global dataset to compose a sub-dataset. In this sub-dataset, any pair of plant and each group of soil biota has the same sampling size. We conduct an additional meta-analysis with this sub-dataset to assess the effects of N enrichment, and conducted a Z-test to compare the effects of N between plant and any group of soil biota.

Both meta-analyses and Q_B test were conducted using the software MetaWin 2.1 (Sinauer Associates, Inc. Sunderland, MA, USA) with a categorical random effect model[89]. The effects of N enrichment were considered significantly positive ($lnRR_+ > 0$, $P < 0.05$) or negative ($lnRR_+ < 0$, $P < 0.05$) if the 95% CIs did not overlap to zero. A significant Q_B indicates that the metrics are significantly different among subgroups[74]. The Z-test was conducted using the equation $Z = \frac{\Delta lnRR}{SE_\Delta}$, where $\Delta lnRR$ represents the difference in the log response ratios ($lnRR$) between plant and soil biota diversity, and SE_Δ is the pooled standard error calculated as $\sqrt{SE_{Plant}{}^2 + SE_{soil}{}^2}$. The test assumes that the compared effect sizes are independent. Statistical significance was determined based on the resulting Z value and corresponding P value, with $P < 0.05$ considered significant[88].

Given that the rate and duration of N treatment varied largely among independent studies within the dataset (Supplementary Table 2), this will lead to significant bias when comparing directly calculated effect size among subgroups (e.g., ecosystem types or climate regions) because this effect size is largely depended on N treatment rate and duration (Supplementary Figs. 11-12).

We thus calculated a standardized effect size (E_{ComN}) of N enrichment at a common rate and duration of N enrichment to eliminate such bias and ensure the effect of N enrichment is comparable across subgroups, and thus to provide a meaningful advance regarding how the effects of N enrichment vary with ecosystem types and climate regions. Prior to calculation, we evaluated the linear and non-linear (logarithmic, quadratic) functions for modeling the effects of N enrichment rate and duration. Our comparison revealed comparable explanatory power across these functions (Supplementary Tables 5-6). To facilitate the standardization of the effect size to a common N enrichment rate and duration, we selected the linear function, but not intend this as an indication that linear function is preferable to non-linear functions. We calculated E_{ComN} as follows:

$$E_{ComN}(\%) = \frac{\exp(lnRR_{+})-1}{R_{+}\times T_{+}} \times 100\% \quad \text{(Eq. 8)}$$

R_{+} and T_{+} are the weighted mean N enrichment rate and duration of a group of ecosystems or climates.

We also calculated the standardized effect size of N enrichment of each paired observation in our dataset with equations 9 and 10, and finally calculated the standardized effect size of each subgroup by conducting a meta-analysis using the software MetaWin 2.1[89].

$$lnRR_{ComN} = \ln\frac{X_N}{X_{CK}} \times \frac{1}{R\times T} = \frac{\ln(X_N)-\ln(X_{CK})}{R\times T} \quad \text{(Eq. 9)}$$

$$Effect\ size_{ComN}(\%) = \frac{X_N - X_{CK}}{X_{CK}\times R\times T} \times 100\% \quad \text{(Eq. 10)}$$

Where R and T are the N enrichment rate and duration of the paired observation.

Our comparison of the results from Eqs. 8, 9 and 10 showed that the standardized effect size for each subgroup from Eq. 8 was significantly positively correlated to the results from Eq. 9 and Eq. 10 (Supplementary Fig. 13). We therefore only reported the results from Eq. 8 because the rate and/or duration of N enrichment is included as influential factors when conducting meta-regression, model selection and structural equation model analyses and global projection for the effect of N enrichment. If we would use results from Eqs. 9 and 10, the rate and duration of N enrichment

would have to be recalculated in these analyses. Given that the calculation on the E_{ComN} was based on the effect size and N enrichment rate and duration, scaling the effect size to a common rate and duration of N treatment does not affect the statistical significance of the effect size.

In our global dataset, the mean, mode, and median N enrichment rates are approximately 100 kg N ha^{-1} $year^{-1}$ (Supplementary Fig. 14). However, the N deposition rate in most parts of the world is currently less than 50 kg N ha^{-1} $year^{-1}$ [79]. In order to link our results to global N deposition, we calculated a standardized effect size of N enrichment at a common rate of 25 kg N ha^{-1} $year^{-1}$ and duration of 10 years.

Meta-regression

We performed mixed-effect meta-regression modeling to examine the relationships of the response ratio (*lnRR*) of N enrichment on plant and soil biodiversity with the rate and duration of N enrichment, *lnRR* of soil mineral N (ammonium and nitrate N) and plant aboveground biomass, and change in pH. Our preliminary analysis showed that N-induced changes in biodiversity metrics were significantly affected by change in soil pH but not by initial soil pH (soil pH in control treatment) (Supplementary Fig. 6). We therefore included pH change rather than initial pH as an influencing factor. We conducted this meta-regression analysis using the lmer function in the *lme4* R package[90] by including "study ID" as a random factor in the model. Given that most variables (9 out of 12) showed no significant relationship with experiment duration (Supplementary Figs. 11-12), we did not include duration as a random effect in our mixed-effect meta-regression models. We then bootstrapped the fitted coefficients by 1000 iterations because many of our models violated the assumption of normality based on the Shapiro-Wilk test on model residuals.

Structural equation modeling

We constructed a structural equation model (SEM) using "piecewise SEM"[91] to examine the direct effects of N enrichment and climate on plant and soil biodiversity and indirect effects

through N enrichment-induced changes in soil properties. In doing this, we selected MAT and aridity index as variables for climate, the changes in soil pH, nitrate and ammonium N concentrations as variables for soil properties. We also selected change in aboveground biomass as variable when examing the effects on plant diversity.

The pathways of the piecewise SEM were fitted as linear mixed-effects models with the study and observation IDs considered as a random factor. We first hypothesized a conceptual model (Supplementary Fig. 15) that included all reasonable pathways, as well as the effect of N and its interaction with each pathway. Tested pathways that were statistically non-significant ($P > 0.05$) were excluded from the model and the model was further optimized to account for more variation. The final optimized model was selected based on the lowest AIC score, and chi-square statistics were run to evaluate the model goodness-of-fit[92]. If the chi-square was statistically non-significant ($P > 0.05$) the model was a good fit to the data. The standardized coefficient for each path from each component model and the Fisher's C and *P* value for the final optimized SEM were displayed in the Fig. 4. All statistical analyses were conducted in the R environment (v4.1.2, http://www.r-project.org/).

Model-selection analysis

We used a model selection and multimodel inference to examine the relative importance of multiple factors influencing the effects of N enrichment on plant and soil biodiversity[93,94]. We conducted this analysis using the *glmulti* R package[95]. The relative importance value of each predictor was calculated as the sum of the Akaike weights (probability that a model is the most plausible model) of the model in which that predictor appears. Hence, predictors with large Akaike weights in the models received a high importance value. These importance values can be considered as the overall support for each variable in the model[96]. We selected 0.8 as the cut-off for importance to differentiate between important and nonessential predictors, according to Terrer et al[94]. A factor with an importance value > 0.8 is generally significant, and a factor with a value

< 0.8 is generally not significant. We examined the relative importance of the influencing factors, including N enrichment rate, N enrichment duration, MAT, AI, change in soil pH and response ratios of soil nutrient concentrations, and plant biomass (only for plant diversity).

We extracted subset databases from the whole dataset based on the indicators of plant and soil biodiversity with the least amount of data and then interpolated the missing data rows for the remaining predictors using the *missRanger* R package[93,97] before conducting structural equation model and model selection analyses. This approach for missing value imputation has often been used in biological studies[98-101]. We conducted missing value imputation for each diversity metric of each group of biodiversity separately.

Data availability

Source data are provided with this paper.

Code availability

Codes for processing the data in this study are provided as Supplementary Code 1.

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Author contributions:

X.W., P.B.R., M.S., G.W., and L.Q. conceptualized the study and developed the methodology; Y.S., X.G., and J.J. collected the data; Y.S., W.K., and X.G. conducted the data analysis; X.W., Y.S., W.K., L.Q., P.B.R., J.P., L.T., M.B., J.M.B., and R.B. discussed and helped to contextualize the results; X.W., Y.S., and W.K. wrote the draft manuscript; X.W., Y.S., W.K., L.Q., G.W., P.B.R., J.P., L.T., M.B., J.M.B., R.B., W.V., X.J., X.W., W.L., Y.H., T.L., Z.C., and Z.K. contributed to reviewing the results, discussion, and editing the paper. L.Q., X.W., P.B.R., M.B., J.P., and J.M.B. provided funding support. X.W. was responsible for project administration.

Competing interests

Authors declare that they have no competing interests.

Table 1| Results of Z-test in comparing effects of nitrogen (N) on plant and any group of soil biota based on Fig. 1. The Z value with a $P < 0.05$ or $P < 0.10$ (two-sided test) indicates significant or marginal significant difference in N effects between plants and soil biota.

Comparison	Biodiversity index	Overall dataset		Ecosystem types				Climate Zones					
				Forest		Grassland		Tropical		Temperate		Boreal	
		Z	P	Z	P	Z	P	Z	P	Z	P	Z	P
Plant vs. soil bacteria	Shannon index	2.87	0.004	0.70	0.480	2.92	0.004	1.78	0.070	0.99	0.320	4.48	<0.001
	Richness	8.06	<0.001	1.77	0.080	5.00	<0.001	1.19	0.240	7.81	<0.001	1.97	0.050
Plant vs. soil fungi	Shannon index	3.40	<0.001	1.08	0.280	3.28	0.001	1.67	0.099	1.36	0.170	5.62	<0.001
	Richness	17.53	<0.001	5.36	<0.001	13.87	<0.001	4.06	<0.001	15.63	<0.001	6.86	<0.001
Plant vs. soil Nematode	Shannon index	0.40	0.690	0.59	0.550	0.39	0.700	1.11	0.270	1.38	0.170	NA	NA

NA: Not applicable

Table 2| Effects of nitrogen (N) enrichment on plant and soil biodiversity with the sub-dataset from the independent studies in our global dataset that include both plant and any group of soil biota (bacteria, fungi, or nematodes). The Z-test is conducted to examine the effects of N enrichment between plants and soils. When the 95% confidence intervals, represented by error bars, do not overlap with zero, the effect is significant at $P < 0.05$ (marked with an *), otherwise, the effect is not significant ($P > 0.05$, marked with ns). The Z value with a $P < 0.05$ (two-sided test) indicates significant significant difference in N enrichment effects between plants and soil biota. The effect sizes (E_{ComN}, %) are standardized to a common rate (25 kg N ha^{-1} $year^{-1}$) and duration (10 years) of N enrichment.

Comparison	Biodiversity index	n[#]	E_{ComN} (%)		Z	P
			Plant	Soil biota		
Plant vs. soil bacteria	Shannon index	40(7)	-11.96%(*)	0%(ns)	6.75	<0.001
	Richness	35(7)	-7.92%(*)	-0.90%(*)	5.37	<0.001
Plant vs. soil fungi	Shannon index	14(5)	-10.06%(*)	3.01%(ns)	6.51	<0.001
	Richness	34(5)	-17.02%(*)	3.28%(*)	6.92	<0.001
Plant vs. soil nematodes	Shannon index	9(3)	-3.23%(ns)	-8.14%(ns)	0.38	0.705

[#]The number of observations and total number of studies are included in the datasets.

Figure Legends

Fig. 1| Effects of nitrogen (N) enrichment on plant and soil biodiversity. Plots show the effect size of N enrichment on richness (**a-c**) and Shannon index (**d-g**) of plant and soil biodiversity across the entire global dataset, within ecosystem types (grasslands, forests, and croplands) and climate regions (tropical, temperate, and boreal). Points and error bars represent mean effect size and 95% confidence (CIs) interval, respectively. The effect sizes (E_{ComN}, %) are standardized to a common rate (25 kg N ha^{-1} $year^{-1}$) and duration (10 years) of N enrichment. When the 95% CIs, represented by error bars, do not overlap with zero, the effect is significant at $P < 0.05$ (marked with solid circles). Otherwise, the effect is not significant ($P > 0.05$; open circles). Black, green and yellow dots indicate the overall dataset, ecosystem types and climates attributes, respectively. The number of observations (n) and total number of studies either across the overall dataset or in each ecosystem and climate category are displayed in parentheses. The plant species richness and Shannon index are not analyzed for croplands because they are highly modified and managed for agricultural purposes. *P* value represents the between group differences based on Cochran's Q test (two-sided tests). Q_B value represents the heterogeneity in effect among groups. The Q_B value with a $P < 0.05$ indicates significant differences in N effects among ecosystem types or climate zones. Source data are provided as a Source Data file.

Fig. 2| Relationships between nitrogen (N) enrichment effects on plant and soil biodiversity versus changes in soil pH and plant biomass. Panels present the relationships between the response ratio (*lnRR*) of plant and soil biodiversity (bacteria, fungi, and nematodes), in terms of richness and Shannon index versus changes in soil pH **(a-c, g-j)**, and *lnRR* of plant aboveground biomass **(d-f, k-n)**, respectively. The relationships are evaluated using two-sided t-tests in mixed-effect meta-regression models, slope and *P* value for each relationship are given, and n represents study observations. The solid line and shaded area are the regression line and its corresponding 95% CIs, respectively. Source data are provided as a Source Data file.

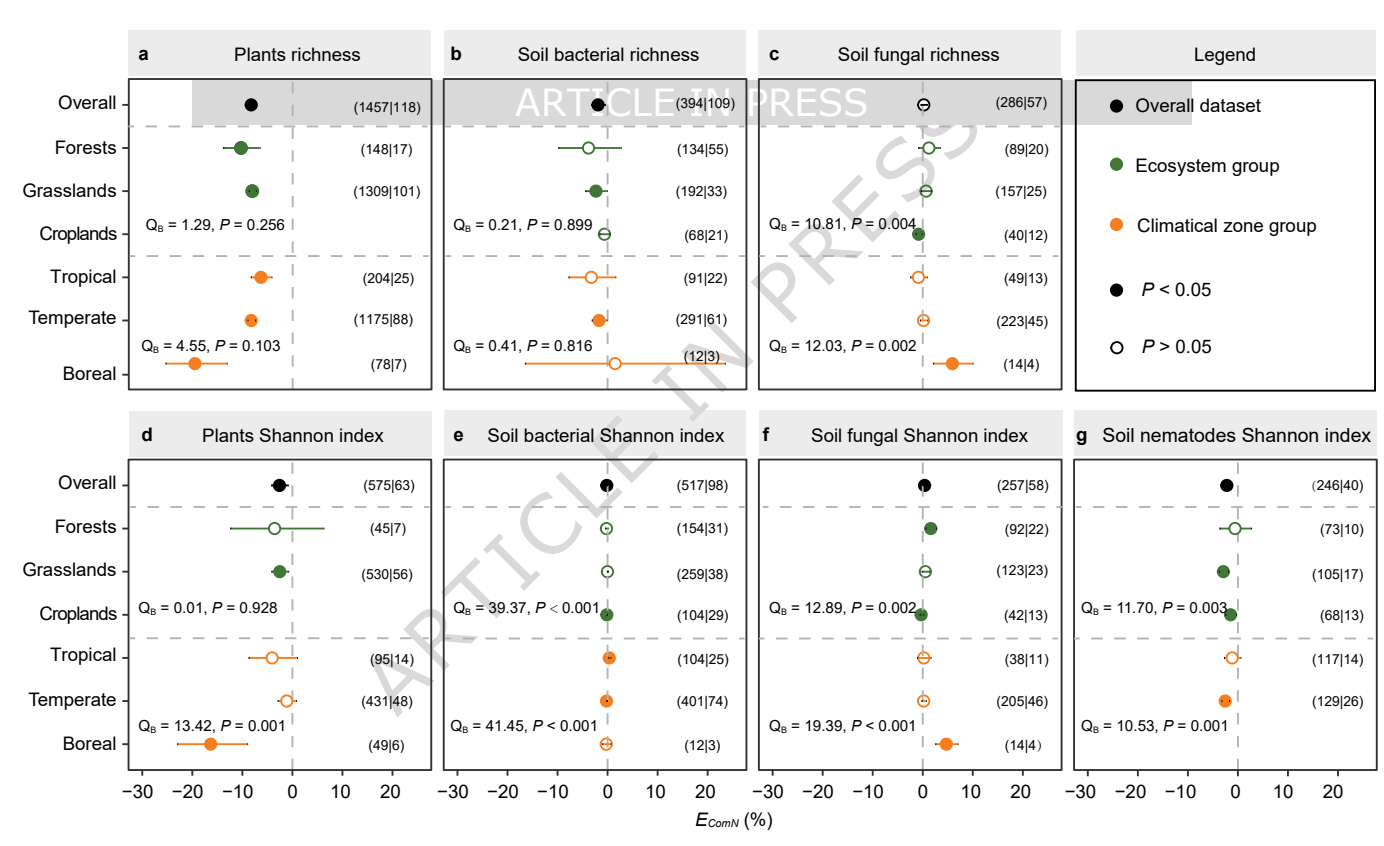
Fig. 3| Comparison in the relationships of changes in biodiversity (response ratio) over nitrogen (N) enrichment rates between plant and soil biota. (a, c) Comparison between plant and soil bacteria. **(b, d)** Comparison between plant and soil fungi. **(e)** Comparison between plant and soil nematodes. The relationships are evaluated using two-sided t-tests in mixed-effect meta-regression models, slope and *P* value for each relationship are given, and n represents study observations. The solid line and shaded area are the regression line and its corresponding 95% CIs, respectively. Blue lines represent the relationships between plant diversity (species richness and Shannon index) and N enrichment rates, whereas red lines represent the relationships for soil biota (bacteria, fungi, and nematodes). *P*-between values indicating differences between the slopes of plant and soil biota responses based on pairwise contrasts of estimated trends (two-sided t-tests). The slopes of the relationship for plant diversity versus N enrichment rates are significantly more negative than slopes of the relationship for soil biota versus N enrichment rates (*P*-between < 0.01). Source data are provided as a Source Data file.

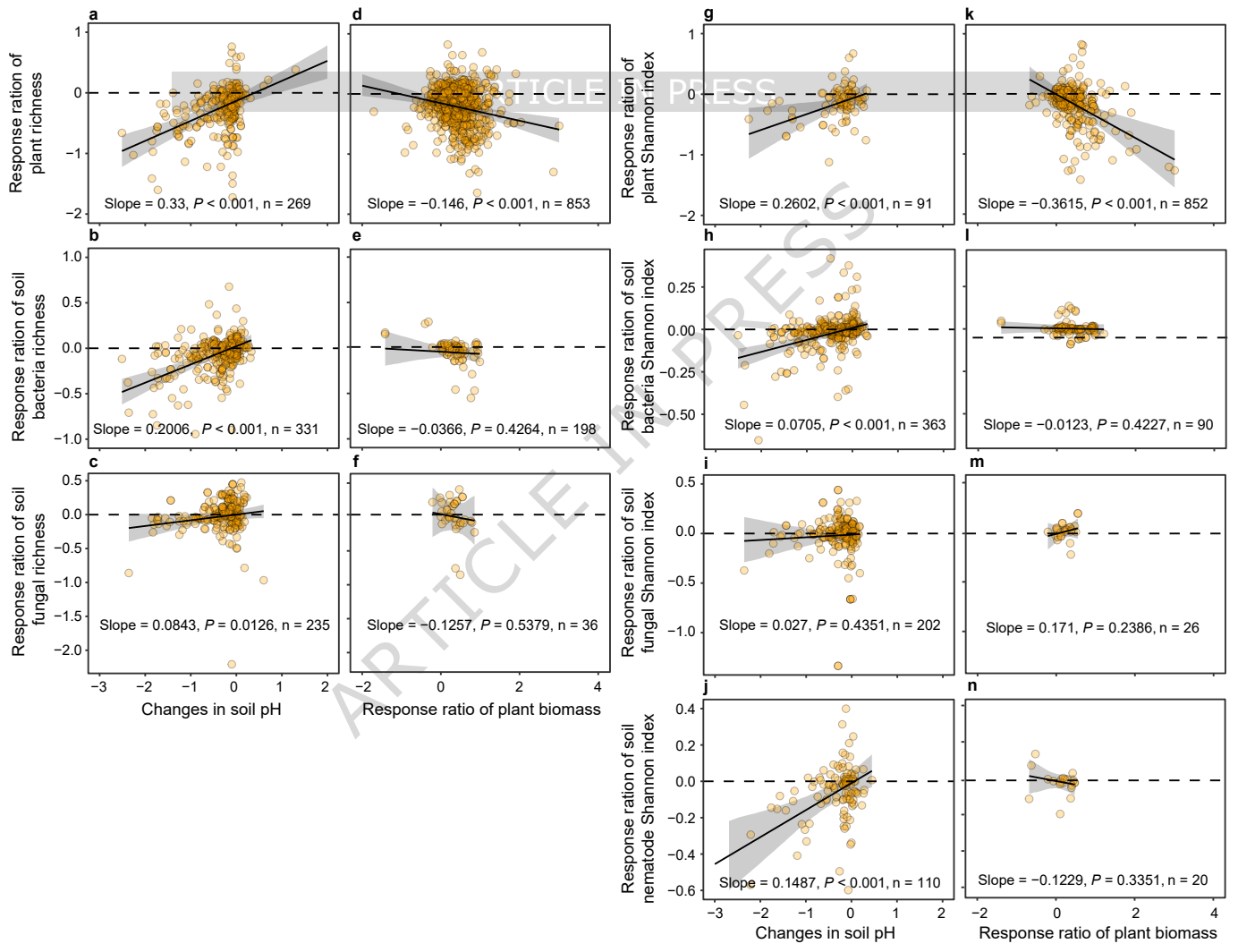
Fig. 4| Pathways regulating nitrogen (N) enrichment-induced changes in plant and soil biodiversity response to N enrichment and climate. Structural equation models showing the pathways through which nitrogen (N) enrichment rate and duration, climate (aridity index and mean annual temperature) and changes in soil properties regulate the N enrichment-induced changes in plant and soil biodiversity. **(a, b)** Plant species richness and Shannon index. **(c, d)** Soil bacterial richness and Shannon index. **(e, f)** Soil fungal richness and Shannon index. **(g)** Soil nematode Shannon index. This analysis is conducted based on a hypothesized conceptual piecewise structural equation model (Supplementary Fig. 15). Red and green lines indicate negative and positive paths ($P < 0.05$), respectively, with the thickness representing the degree of influence. Numbers adjacent to arrows are standardized path coefficients. The conditional R^2 (R_c^2) denotes the variance explained by both fixed and random effects of "Study ID" and "Observation

ID", whereas the marginal R^2 (R_m^2) denotes the variance explained by fixed effects in the linear mixed-effects models. Statistical significance is based on Fisher's C tests (two-sided), and n represents study observations. The N enrichment-induced changes in plant and soil properties are present as response ratio (*lnRR*), while the change in soil pH is present as a difference between N enrichment and control treatments. Source data are provided as a Source Data file.

Fig. 5| Model-averaged importance of predictors for effects of nitrogen(N) enrichment on plant and soil biodiversity based on Akaike information criteria. The relative importance of nitrogen (N) enrichment rate and duration, climate (mean annual tempertaure, and aridity index), nitrogen (N) enrichment-induced changes in soil nutrients (ammonium and nitrate), pH and plant diversity (richness and Shannon index) and aboveground biomass on effects of N enrichment on plant and soil biodiversity based on the cumulative sum of Akaike weights derived from the model selection using corrected Akaike's information criteria. **(a, b)** Plant species richness and Shannon index. **(c, d)** Soil bacterial richness and Shannon index. **(e, f)** Soil fungal richness and Shannon index. **(g)** Soil nematode Shannon index. The dashed lines present the importance value of 0.8, which is selected as the cut-off value of importance to differentiate important and non-essential predictors according to Terrer et al. (*94*). Variables with a dashed line exceeding 0.8 is considered important, based on the entire dataset observations (n = 3816). Source data are provided as a Source Data file.

Editorial Summary
Addressing how the nitrogen-induced changes in plant diversity differ from those in soil organisms is critical. This global meta-analysis suggests that nitrogen enrichment has stronger negative effects on plant diversity but modest to negligible effects on soil bacterial and fungal diversity.
Peer Review Information: *Nature Communications* thanks Harry Olde Venterink, Mark Nessel and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. A peer review file is available.




a
Response ration of plant richness
Slope = 0.33, P < 0.001, n = 269
d
Slope = −0.146, P < 0.001, n = 853
g
Response ration of plant Shannon index
Slope = 0.2602, P < 0.001, n = 91
k
Slope = −0.3615, P < 0.001, n = 852
b
Response ration of soil bacteria richness
Slope = 0.2006, P < 0.001, n = 331
e
Slope = −0.0366, P = 0.4264, n = 198
h
Response ration of soil bacteria Shannon index
Slope = 0.0705, P < 0.001, n = 363
l
Slope = −0.0123, P = 0.4227, n = 90
c
Response ration of soil fungal richness
Slope = 0.0843, P = 0.0126, n = 235
f
Slope = −0.1257, P = 0.5379, n = 36
i
Response ration of soil fungal Shannon index
Slope = 0.027, P = 0.4351, n = 202
m
Slope = 0.171, P = 0.2386, n = 26
j
Response ration of soil nematode Shannon index
Slope = 0.1487, P < 0.001, n = 110
n
Slope = −0.1229, P = 0.3351, n = 20
Changes in soil pH
Response ratio of plant biomass
Changes in soil pH
Response ratio of plant biomass
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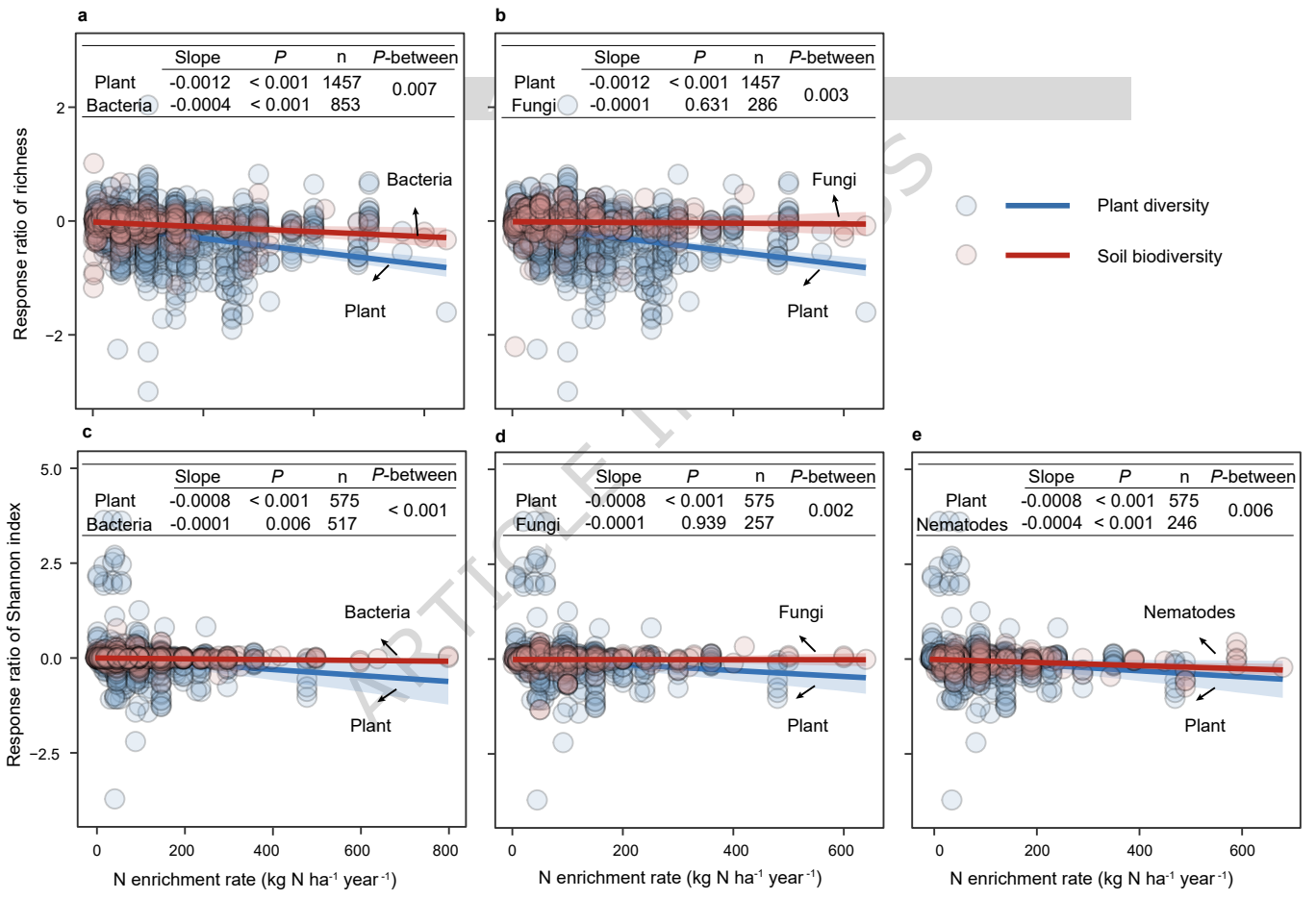
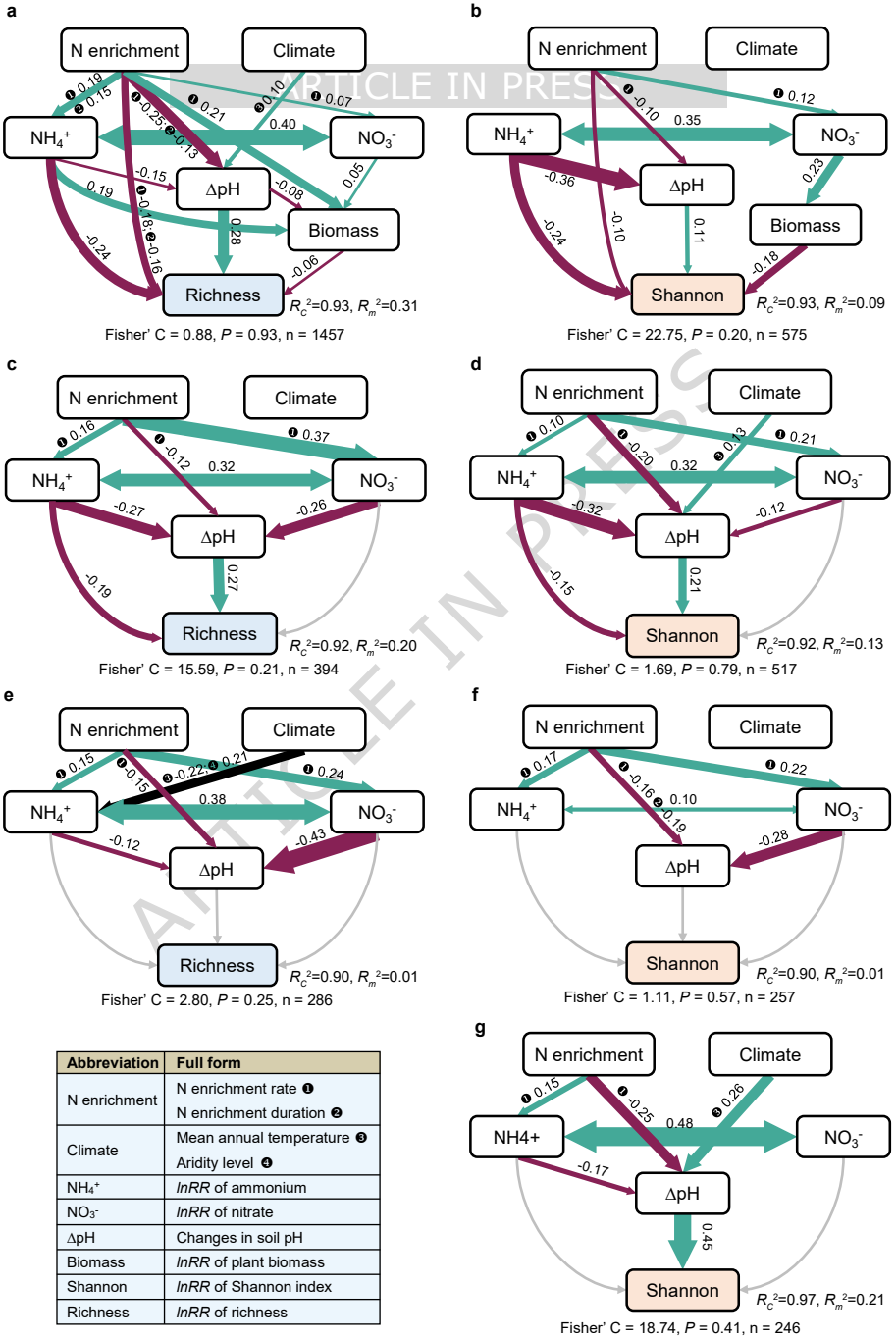

a
b
c
d
e
Slope P n P-between
Plant -0.0012 < 0.001 1457 0.007
Bacteria -0.0004 < 0.001 853
Plant -0.0012 < 0.001 1457 0.003
Fungi -0.0001 0.631 286
Plant -0.0008 < 0.001 575 < 0.001
Bacteria -0.0001 0.006 517
Plant -0.0008 < 0.001 575 0.002
Fungi -0.0001 0.939 257
Plant -0.0008 < 0.001 575 0.006
Nematodes -0.0004 < 0.001 246
Bacteria
Fungi
Nematodes
Plant
Plant diversity
Soil biodiversity
Response ratio of richness
Response ratio of Shannon index
N enrichment rate (kg N ha-1 year-1)



Abbreviation	Full form
N enrichment	N enrichment rate ❶ N enrichment duration ❷
Climate	Mean annual temperature ❸ Aridity level ❹
NH_4^+	*lnRR* of ammonium
NO_3^-	*lnRR* of nitrate
ΔpH	Changes in soil pH
Biomass	*lnRR* of plant biomass
Shannon	*lnRR* of Shannon index
Richness	*lnRR* of richness