Received: 16 January 2022 | Revised: 18 July 2022 | Accepted: 18 July 2022

DOI: 10.1111/gcb.16361

Global Change Biology WILEY

RESEARCH ARTICLE

Nitrogen fertilization weakens the linkage between soil carbon and microbial diversity: A global meta-analysis

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Funding information
the National Natural Sciences Foundation of China, Grant/Award Number: 42107282; Western light Foundation of the Chinese Academy of Sciences, Grant/Award Number: XAB2019B11; Open Fund of State Key Laboratory of Loess and Quaternary Geology, Grant/Award Number: SKLLQG1915; Natural Science Foundation of Shanxi Province, Grant/Award Number: 2021JM-213; Strategic Priority Research Program of Chinese Academy of Science, Grant/Award Number: XDB40020203

Abstract

Soil microbes make up a significant portion of the genetic diversity and play a critical role in belowground carbon (C) cycling in terrestrial ecosystems. Soil microbial diversity and organic C are often tightly coupled in C cycling processes; however, this coupling can be weakened or broken by rapid global change. A global meta-analysis was performed with 1148 paired comparisons extracted from 229 articles published between January 1998 and December 2021 to determine how nitrogen (N) fertilization affects the relationship between soil C content and microbial diversity in terrestrial ecosystems. We found that N fertilization decreased soil bacterial (−11%) and fungal diversity (−17%), but increased soil organic C (SOC) (+19%), microbial biomass C (MBC) (+17%), and dissolved organic C (DOC) (+25%) across different ecosystems. Organic N (urea) fertilization had a greater effect on SOC, MBC, DOC, and bacterial and fungal diversity than inorganic N fertilization. Most importantly, soil microbial diversity decreased with increasing SOC, MBC, and DOC, and the absolute values of the correlation coefficients decreased with increasing N fertilization rate and duration, suggesting that N fertilization weakened the linkage between soil C and microbial diversity. The weakened linkage might negatively impact essential ecosystem services under high rates of N fertilization; this understanding is important for mitigating the negative impact of global N enrichment on soil C cycling.

KEYWORDS
bacteria, fungi, global change, soil organic C, terrestrial ecosystem

1 | INTRODUCTION

Soil microbes comprise a large portion of the genetic diversity and affect carbon (C) cycling in terrestrial ecosystems (Allison & Martiny, 2008; Bahram et al., 2018; Li et al., 2021; Singh et al., 2004; Thompson et al., 2017). Soil microbial diversity plays a major role in ecosystem function ranging from microbial metabolism to C and nutrient cycling. Soil microbial diversity is often tightly coupled to soil

C accumulation through microbial controls on C cycling (Delgado-Baquerizo et al., 2013; Luo et al., 2022; Singh et al., 2010). Recently, the positive role of microbes in soil C storage through the "microbial carbon pump" (MCP) has been emphasized (Liang et al., 2017). Two pathways, including *ex vivo* modification and *in vivo* turnover, affect microbial catabolism and/or anabolic soil C dynamics (Liang et al., 2019; Wang et al., 2021). The "MCP" theory suggests that the microbial formation of multiple organic compounds is tightly coupled, and through which soil C is stabilized.

Nitrogen (N) is an essential nutrient for plant and microbial growth (Elrys, Ali, et al., 2021; Elrys et al., 2022; Niu et al., 2016; Yu et al., 2019). With the rapid development of modern industry and agriculture, anthropogenic activities such as fossil fuel combustion and N fertilization (mainly organic [urea] and inorganic N fertilizers) have substantially enhanced N inputs into soils (Bahram et al., 2018; Kuypers et al., 2018). In natural ecosystems, available N for plants and microbes mainly comes from soil N mineralization and external N inputs, such as atmospheric N deposition and biological N-fixation (Li, Wang, et al., 2020; Li, Zeng, et al., 2020; Yu et al., 2019). In managed ecosystems, available N for plants and microbes mainly comes from N fertilization (Carrara et al., 2018; Li et al., 2019; Louca et al., 2018). Nitrogen deposition and fertilization are important sources of N that alleviate N limitations in terrestrial ecosystems on a global scale (Elrys, Ali, et al., 2021; Elrys et al., 2022; Yu et al., 2019). The rate of atmospheric N deposition has been predicted to increase by 2.5 times worldwide in the next century (IPCC, 2014). Increased N deposition and N fertilization increase N losses to the environment. For example, recent meta-analysis studies showed that increased N input increases the potential risk of N loss in different ecosystems (Chen et al., 2019; Elrys et al., 2022; Yu et al., 2019), and the N imbalance will become worse in the future.

Extensive research has shown that N enrichment decreases plant and microbial diversity in different terrestrial ecosystems (Niu et al., 2016; Philippot et al., 2013; Singh et al., 2010; Zhang et al., 2018), and the negative effect is aggravated by an increasing rate of N fertilization (Chen et al., 2019; Wang, Lu, et al., 2018; Yang et al., 2020, 2021). As soil N enhancement increases, more protons (H^+) are released into the soil due to increased nitrification (NO_3^-) and plant uptake of ammonium (NH_4^+) (Wang, Lu, et al., 2018; Zhang et al., 2018; Zhou et al., 2017; Zhu et al., 2018). Increased proton production enhances the mobilization of aluminum ions that can be toxic to plants and microbes, leading to a decline in plant and microbial diversity (Geisseler et al., 2017; Lange et al., 2015; Wang, Lu, et al., 2018; Ye et al., 2018; Zhu et al., 2018). N fertilization enhances soil N availability (Buchkowski et al., 2017; Tripathi et al., 2018; Zhalnina et al., 2015) and increases plant productivity and the associated C input (Liang et al., 2017; Wang, Liu, & Bai, 2018). Nitrogen input can stimulate the production of plant and root biomass (Chen et al., 2019; Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Prommer et al., 2020), root exudation of C, and benefit soil organic C (SOC) accumulation (Chen et al., 2019; Xu, Xu, et al., 2021; Xu, Li, et al., 2021). In fact, the effects of N fertilization on SOC are often variable, with positive, negative, or neutral impacts due to the dynamic balance between C inputs and effluxes across study sites (Eastman et al., 2021; Feng et al., 2022; Lu, Hou, et al., 2021). A meta-analysis study showed that although N addition substantially increased the aboveground biomass (more than 35%) and organic matter input to soil, and soil C storage was not significantly enhanced by N addition in forests or grasslands (Li et al., 2016). One of the mechanisms of the N-induced increase in SOC is the increased plant productivity (Gurmesa et al., 2022; Schulte-Uebbing et al., 2022). However, increased N availability could also increase plant litter decomposability (Carrara et al., 2018; Doetterl et al., 2018), resulting in more rapid soil C decomposition, offsetting the effect on soil C accumulation from the increased plant productivity under N fertilization, making it possible for either SOC to be decreased or increased (Lundberg & Teixeira, 2018; Zhou et al., 2017).

Soil dissolved organic C (DOC) and microbial biomass C (MBC) represent labile C forms that turn over fast in soil and play crucial roles in terrestrial soil C cycling (Guo et al., 2020). Nitrogen fertilization could alter SOC by changing the dynamics of DOC and MBC (Zhang et al., 2020). Previous meta-analysis reported that N addition enhanced DOC and MBC by more than 110% and 10%, respectively (Zhou et al., 2017). While the mechanisms driving changes in SOC under N fertilization has been widely documented, the responses of DOC and MBC to N fertilization and their contribution to SOC are still unclear.

Previous studies showed that the diversity of soil microbial community decreases with decreasing soil C content (Dai et al., 2018; Wang, Lu, et al., 2018; Wu et al., 2021; Xia & Wan, 2008; Yang et al., 2017; Zhang et al., 2018), although the implications of this relationship for microbial processes are unknown. Soil microbial diversity and C content are often tightly coupled; however, the relationships can be affected by N fertilization. Our understanding of the linkage between microbial diversity and soil C content (including SOC, DOC, and MBC) due to N fertilization is very limited (Allison & Martiny, 2008; Li et al., 2019). Here, we propose a mechanistic framework (Figure 1) to understand how N fertilization may affect relationships between soil microbial diversity and soil C content. Based on this framework, we hypothesize that N fertilization would decrease soil microbial diversity but increase soil C content, and thus weaken the linkage between microbial diversity and soil carbon. We collected 1148 paired data points (fertilized vs. nonfertilized control) from 229 articles to study how N fertilization, including the fertilization rate, type, and experimental duration, affects soil microbial diversity and C dynamics in different terrestrial ecosystems.

2 | META-ANALYSIS

2.1 | Data sources

We searched for articles in Web of Science, Google Scholar, ScienceDirect, PubMed, and CNKI (China National Knowledge Infrastructure) that were published between January 1998 and December 2021 using search terms "N fertilization/enrichment/application/amendment and soil microbial diversity," "N fertilization/

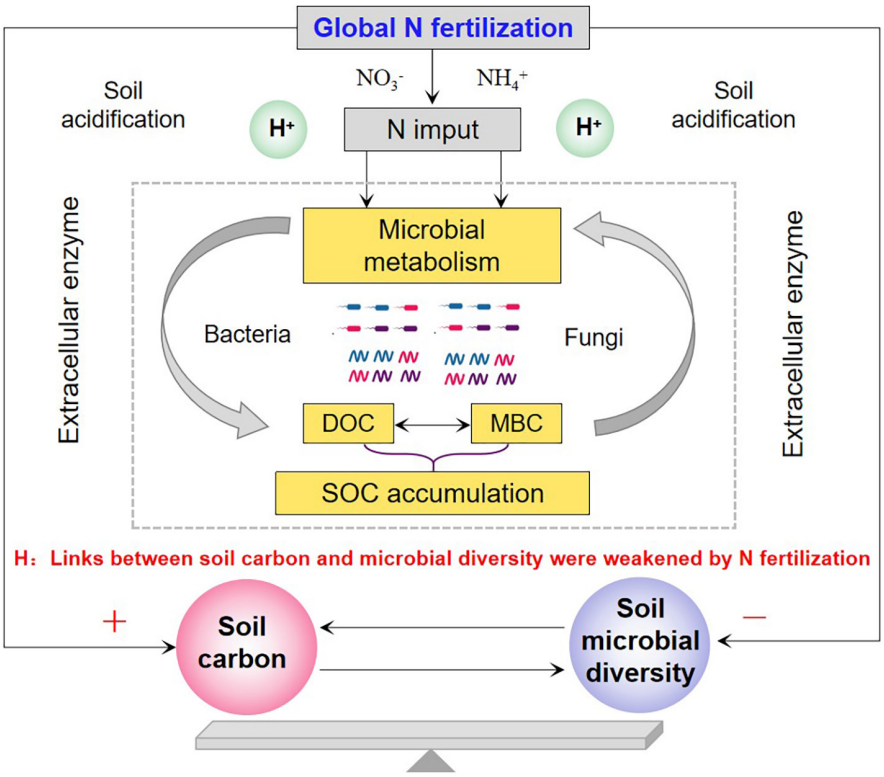

FIGURE 1 A mechanistic framework describing the effect of N fertilization on the relationship between soil C and microbial diversity. Soil released more protons (H^+) due to increased nitrification (NO_3^-) and the absorption of ammonium (NH_4^+) from N inputs, which enhanced C and N availability. In this case, SOC sequestration enhanced by the soil microbial carbon pump and soil microbial assimilation C efficiency. However, soil acidification decreased soil microbial diversity, and thus, N fertilization decouples microbial diversity and soil C content at the global scale. [Colour figure can be viewed at wileyonlinelibrary.com]

enrichment/application/amendment and soil microbial communities," and "N fertilization/enrichment/application/amendment and soil organic carbon or dissolved organic carbon." Our meta-analysis only included data from the surface mineral soil layer in different ecosystems.

For a study to be included for this meta-analysis, it must meet the following criteria: (1) The experiment was conducted in the field, with at least one pair of data (control and N fertilization treatment), with methods including Illumina MiSeq, denatured gradient gel electrophoresis [DGGE], phospholipid fatty acids [PLFA], Roche 454 sequencing technique, and terminal restriction fragment length polymorphism [T-RFLP] used to study soil microbial diversity, and SOC and DOC data; (2) the control (CK) and N fertilization treatment plots had the same condition (i.e., microclimate, soil property, and vegetation type); (3) the N fertilization experiment was conducted in terrestrial ecosystems, with the experimental duration and rate of N fertilization data also collected; (4) the field experiment was conducted for at least one whole growing season; (5) if the field experiment from the same article was conducted in different ecosystems, each study was considered independent; and (6) the mean, standard deviation, or standard error, as well as sample size for the variables were collected whether they were given in the text, tables, or figures. The Shannon index was used as an indicator for soil microbial diversity in this meta-analysis.

Based on the above-mentioned criteria, we collected 1148 paired observations from 229 articles (Figure S1). The type of the ecosystem, N fertilization regime (including the experimental duration and N fertilization rate), and N fertilization type (NH_4-N, NO_3-N, urea) data were collected from each study. Data presented in figures were extracted by the Getdata 2.25 software (https://getdata-graph-digitizer.com/). In addition, plant biomass (aboveground biomass [AGB, $g\,m^{-2}$], litter mass [$g\,m^{-2}$], root biomass [$g\,m^{-2}$]), soil properties, including SOC ($g\,kg^{-1}$), DOC ($mg\,kg^{-1}$), soil total N (STN, $g\,kg^{-1}$), soil MBC ($mg\,kg^{-1}$), soil pH, mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), latitude, and longitude (https://www.worldclim.org/), were collected for each study. To obtain climate data that are not available in the literature, MAP and MAT were extracted from the National Climatic Data Center (https://www.ncdc.noaa.gov/) or WorldClimate (https://www.world climate.com). Finally, we divided these N fertilization experiments into different groups based on the duration of N fertilization (<5, 5–10, 10–20, and >20 years), rate of N fertilization (<50, 50–100, 100–200, and >200 $kg\,ha^{-1}\,year^{-1}$), the type of N fertilization (NH_4-N, NO_3-N, urea), or ecosystem type (forestland, shrubland, grassland, cropland, and tundra).

2.2 | The meta-analysis of response ratios

The natural logarithm-transformed response ratio [ln (RR)] was used to examine how N fertilization affected soil microbial attributes (Hedges et al., 1999). The effect size in an individual observation (d_{ij}) was calculated by the following formula:

$$d_{ij} = \ln\left(RR_{ij}\right) = \ln\left(Y_t / Y_c\right) = \ln Y_t - \ln Y_c, \quad (1)$$

where d_{ij} is the effect size in an individual observation, Y_t is the average value for the N fertilization treatment, and Y_c is the average value for the control (CK).

Sampling variance (V_{ij}) in an individual observation was calculated as follows (Bornstein et al., 2011; Hedges et al., 2010):

$$V_{ij} = \frac{S_t^2}{N_t Y_t^2} + \frac{S_c^2}{N_c Y_c^2}, \quad (2)$$

where N_c and N_t are the number of samples in the control and N fertilization treatments, respectively, and S_c and S_t are the standard deviations for control and N fertilization treatments, respectively.

A nonparametric weighting function was applied in individual weighting research (Bates et al., 2013). The weighting factor (W_{ij}) of an individual observation was calculated as follows:

$$W_{ij} = 1 / V_{ij}, \quad (3)$$

If many observations were made at the same site, weightings had to be adjusted based on the total number of observations in each group (n). V_n is the weight of group (n). Accordingly, the final weight (W_{ij}') was calculated as follows:

$$W_{ij}' = W_{ij} / V_n \quad (4)$$

For each microbial variable, we tested whether the overall ln RR differed from zero and whether the ln RR was affected by N fertilization rate (F, kg ha^{-1} year^{-1}) and experimental duration (D, year) using the following linear mixed effects model:

$$\ln \mathrm{RR} = \beta_0 + \beta_1 \times F + \beta_2 \times \ln(D) + \pi_{\mathrm{study}} + \varepsilon, \quad (5)$$

where β, π_{study}, and ε are coefficient, the random effect factor of "study" and sampling error, respectively. β_0 is the overall lnRR at the mean F and ln(D). The random effect explicitly accounts for autocorrelation among observations within each "study." We applied linear mixed effects models using the restricted maximum likelihood estimation with the lme4 package (Zimlichman et al., 2013). Continuous predictors, that is, N and ln(D) in Equation (5), were centered or scaled the observed value minus mean and divided by one standard deviation. To facilitate the comparison among microbial variables that had variable N and ln(D), we scaled these predictors by using Akaike information criterion (AIC) in our analysis. We also tested four other alterative models, but all alternative models resulted in similar or greater AIC values (Table S1) and are thus not presented in this paper.

2.3 | Meta data analyses

We used METAWIN 2.1.3 (https://www.metawinsoft.com, Sinauer Associates Inc.) to calculate the effect size. For ease of interpretation, lnRR and its corresponding confidence intervals (CIs) were the effect size. If the 95% CI of lnRR does not overlap with zero, the effect of N fertilization on the variable is significant at $\alpha = 0.05$, similar to most previous meta-analyses (Chen & Chen, 2019; Limpens et al., 2011, 2012; Wang, Lu, et al., 2018; Yuan & Chen, 2015). For each effect size, we calculated the corresponding 95% CIs using the bootstrap approach with $n = 999$ iterations and examined whether the 95% CIs overlap with 0. If the 95% CIs do not overlap with 0, the effect size is significant at $p < 0.05$ (Arnqvist & Wooster, 1995; Gurevitch et al., 2001). Furthermore, total heterogeneity (Q_T), residual error (Q_E), and heterogeneity in cumulative effect sizes (Q_M) were calculated (Cheng et al., 2019; Lajeunesse, 2011; Limpens et al., 2011). The Q value denotes χ^2 distribution, involving a significance test for the null hypothesis. Subsequently, the publication bias was tested for soil microbial diversity, and the significance of the correlation coefficient suggests the potential presence of publication bias (Arnqvist & Wooster, 1995; Gurevitch et al., 2001). In addition, the relative frequency of plant biomass (including AGB, litter, root), soil microbial diversity, SOC, MBC, DOC, and soil properties (STN, pH) were found to be normally distributed (Figure S2). Moreover, the residual error (Q_E) and total heterogeneity (Q_M) in an individual observation were computed according to the χ^2 distribution (Tables S2 and S3); in the meantime, we analyzed publication bias by using the "funnel" function of the R package metafor and used the modification of the Egger's test proposed by Nakagawa and Santos (2012) to assess funnel plots' asymmetry of the null models' residuals (Tables S4 and S5).

2.4 | Statistical analyses

Statistical analysis was conducted in three steps. First, Pearson's correlation coefficients between plant biomass and soil microbial diversity, SOC, MBC, or DOC were determined and illustrated using a heat map. Those analyses were performed using the "complexheatmap" package in R.

Second, we evaluated how the relationships between the response ratios of soil microbial diversity and SOC, MBC, or DOC change with N fertilization rate and experimental duration. We tested the effects of N fertilization rate and experimental duration on Pearson's correlation coefficients by replacing the terms of lnRR in Equation (5) with correlation coefficients. Box plots with the correlation coefficients (obtained from each individual observation by Pearson correlation analysis) were used to graphically demonstrate the dependence of relationships among soil microbial diversity and SOC, MBC, or DOC on N fertilization rate and experimental duration. These box plots were made using the "ggplot" package in R software v. 4.0.2 (http://www.datavis.ca/R/).

Finally, to mechanistically understand the N fertilization effect on the response ratio of soil microbial diversity, SOC, MBC, and DOC, we developed a structural equation modeling (SEM) using the "piecewiseSEM" package to account for the random effects of "study site" (Chen et al., 2022; Elrys, Ali, et al., 2021; Elrys, Wang, et al., 2021). We selected the final model and evaluated the R^2 values, which represent the amount of variation explained by variables, calculated after 999 bootstraps. There were low chi-square

coefficients (χ^2), nonsignificant ($p > .05$) and large goodness of fit (GFI) (>.90), low AIC, and low root mean square error of the approximation (RMSEA) (<.05). Our results indicate that model fitted our data very well.

3 | RESULTS

3.1 | Nitrogen fertilization effects on soil C and microbial diversity

Across all observations, N fertilization significantly decreased bacterial diversity (mean effect size −0.11, with the 95% CI ranging from −0.19 to −0.03), fungal diversity (−0.17, −0.21 to −0.14) (Figure 2), soil pH (−0.23, −0.26 to −0.20), but significantly increased SOC (0.19, 0.12–0.26), MBC (0.17, 0.12–0.21), and DOC (0.25, 0.22–0.28), without affecting STN (Figure 2). In addition, N fertilization significantly increased AGB (0.11, 0.07–0.15), litter mass (0.16, 0.11 to 0.21), and root biomass (0.21, 0.14–0.28).

The N fertilization effect on bacterial and fungal diversity was dependent on the ecosystem type, N fertilizer type, and fertilization rate and duration (Figure 3). Nitrogen fertilization decreased bacterial and fungal diversity in croplands and grasslands, increased their diversity in forestlands, but did not affect their diversity in shrublands or tundra. The 95% CI for the response ratio ranged between −0.07 and 0.02 for bacterial diversity, and −0.09 and 0.03 for fungal diversity among the different experimental duration groups. Moreover, the 95% CI for the response ratio of fungal diversity ranged between −0.05 and −0.02 and the response ratio reached its maximum (most negative) value (absolute) when the N fertilization rate was 50–100 kg ha^{-1} year^{-1} (Figure 3). The most negative effect on bacterial and fungal diversity occurred in the 5–10 year group and the negative effect (absolute value) decreased as the experimental duration increased (Figure 3). Among different ecosystem types, the response ratio of soil microbial diversity gradually decreased with N fertilization rate and experimental duration, with threshold values of 100 kg ha^{-1} year^{-1} and 10 years, respectively (Figure 4).

The N fertilization effect on SOC, MBC, and DOC was also dependent on the ecosystem type, N fertilizer type, and fertilization rate and duration (Figure 3). Nitrogen fertilization increased SOC in croplands and grasslands but not in shrublands, forestlands, and tundra. However, N fertilization decreased DOC in croplands but increased DOC in grasslands, shrublands, and forestlands. The response ratios for SOC, MBC, and DOC were positive when the N fertilization rate was 50–100 kg ha^{-1} year^{-1} and when the experimental duration was less than 10 years; in contrast, N fertilization did not affect SOC, MBC, and DOC when the N fertilization rate was less than 50 kg ha^{-1} year^{-1} or when the experimental duration was longer than 10 years (Figure 3). Among different ecosystem types, the response ratios of SOC, MBC, and DOC gradually increased with N fertilization rate and experimental duration, with thresholds of 100 kg ha^{-1} year^{-1} and 10 years, respectively (Figure 4).

Organic N (urea) fertilization increased MBC and DOC, but decreased microbial diversity, while inorganic N fertilization (NH_4-N and NO_3-N) decreased MBC and DOC, but increased soil microbial diversity (Figure 3). The absolute value of the coefficients was greater with organic N than with inorganic N fertilization.

3.2 | Linkage between soil C and microbial diversity under N fertilization

Across all observations, SOC, MBC, and DOC were negatively related to ($p < .05$) soil bacterial and fungal diversity (Figure 5), while the absolute values of these relationships gradually decreased with the increasing N fertilization rate and experimental duration (Figure 6). Moreover, MBC and DOC were positively related to SOC ($p < .05$) (Figure S3). However, the absolute values of these

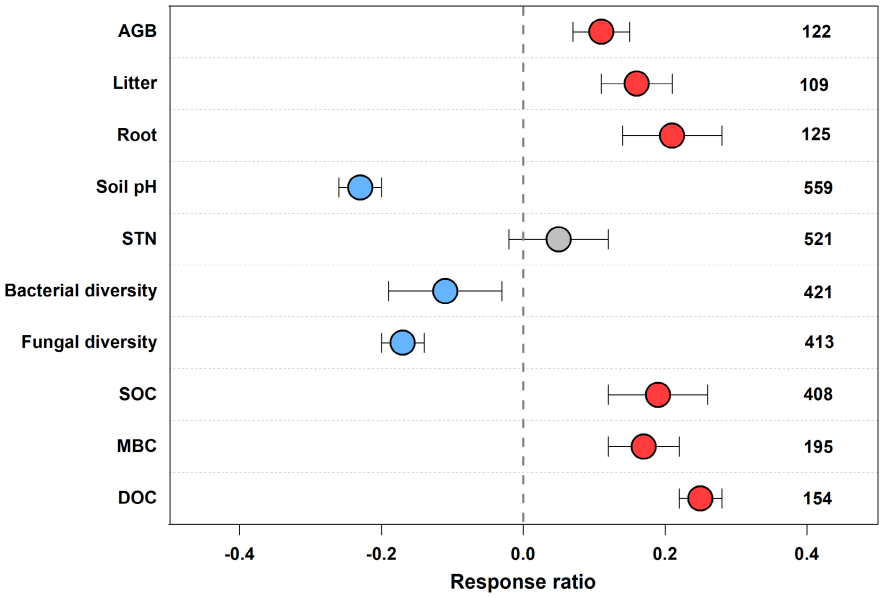

FIGURE 2 Effects of N fertilization on soil microbial diversity, SOC, MBC, DOC, STN, and plant biomass. AGB, aboveground biomass; DOC, dissolved organic carbon; MBC, soil microbial biomass carbon; SOC, soil organic carbon; STN, soil total nitrogen. [Colour figure can be viewed at wileyonlinelibrary.com]

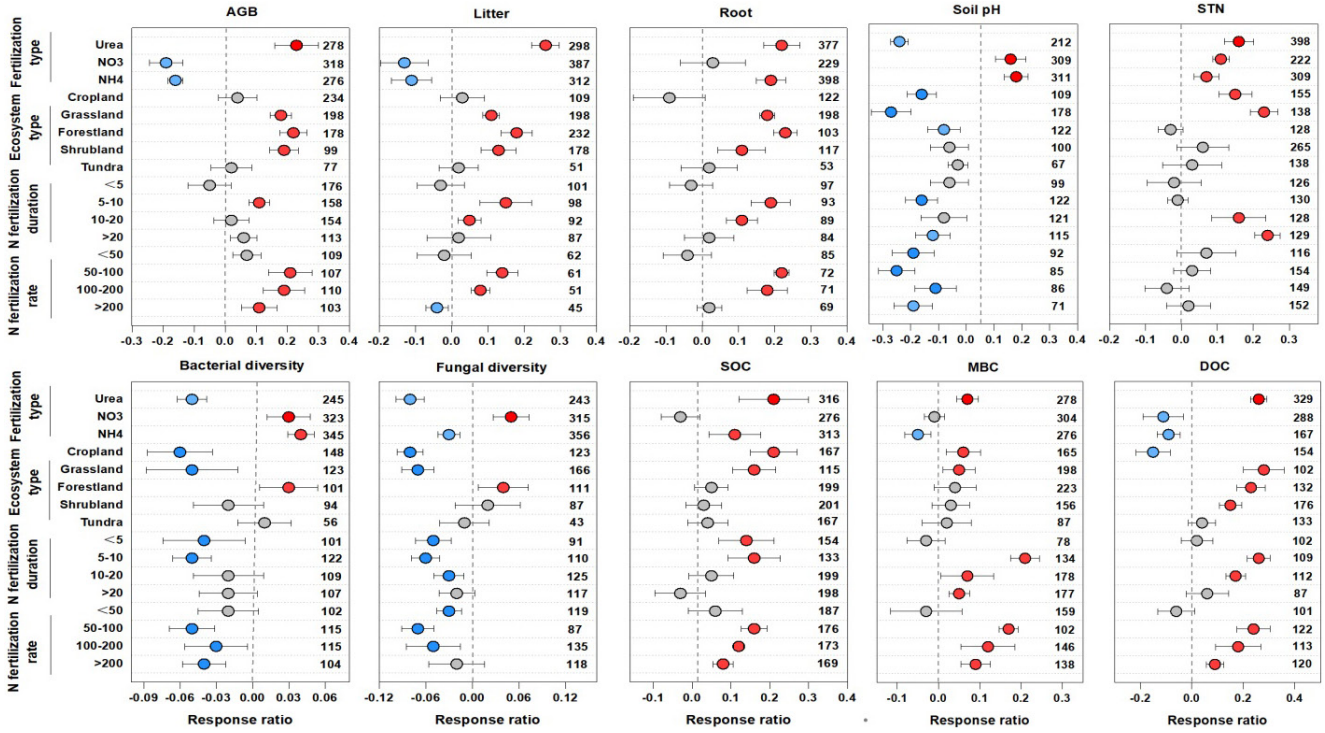

FIGURE 3 The effects of N fertilization on the response ratios (lnRR) of soil microbial diversity, SOC, MBC, DOC, STN, and plant biomass based on ecosystem type, N fertilization type, N fertilization rate (kg ha^{-1} year^{-1}), and duration (years). Values are mean ± 95% confidence intervals of the percentage effects between the N fertilization and control treatments. Gray symbols have no significant difference, and blue symbols are negative, and red symbols are positive means whose confidence intervals do not include zero. AGB, aboveground biomass; DOC, dissolved organic carbon; MBC, soil microbial biomass carbon; SOC, soil organic carbon; STN, soil total nitrogen. [Colour figure can be viewed at wileyonlinelibrary.com]

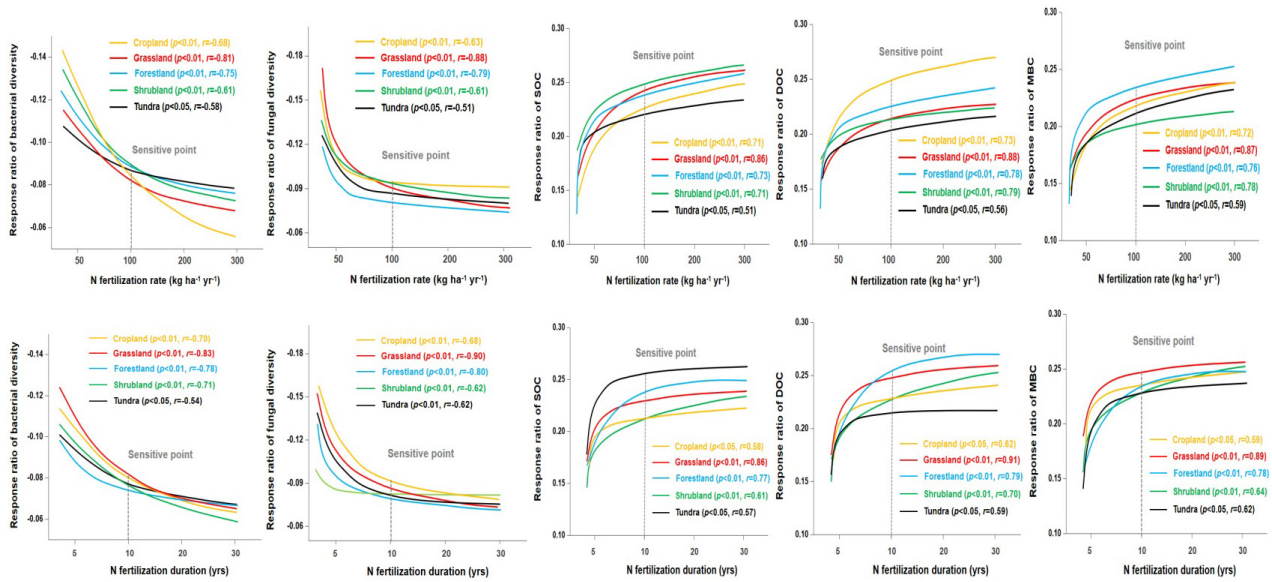

FIGURE 4 Effects of N fertilization rate (kg ha^{-1} year^{-1}), and duration (years) on the response of soil microbial diversity, soil organic carbon (SOC), microbial biomass carbon (MBC), dissolved organic carbon (DOC) across different ecosystem types. [Colour figure can be viewed at wileyonlinelibrary.com]

relationships gradually decreased with the increasing N fertilization rate and experimental duration (Figure S4). Soil microbial diversity was negatively related to AGB and root biomass, and soil pH was also negatively related to AGB, litter mass, and root biomass. Yet, SOC and DOC were positively related to AGB, litter mass, and root biomass (Figure S3).

We constructed an SEM to explain how environmental factors affected soil microbial diversity and C content (Figure 7). The final SEM

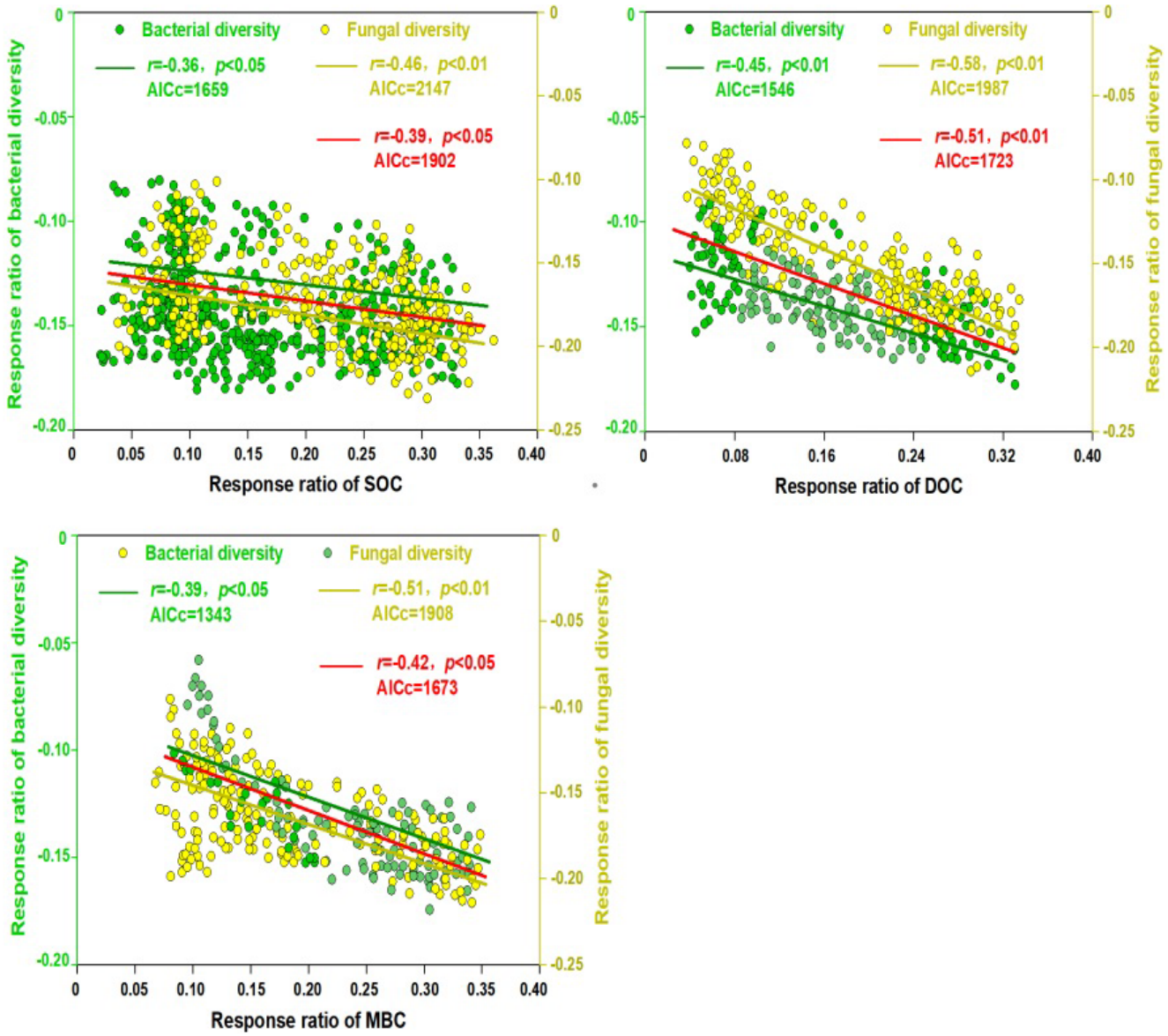

FIGURE 5 Soil microbial diversity is significantly related to soil organic carbon (SOC), microbial biomass carbon (MBC), dissolved organic carbon (DOC), and the best polynomial fit were determined on the basis of the corrected Akaike information criterion (AIC). [Colour figure can be viewed at wileyonlinelibrary.com]

explained 78% of the variance for soil microbial diversity (p = .62, χ^2 = 5.6, CFI = 0.96, AIC = 154, RSMEA = 0.002). Nitrogen fertilization increased DOC, MBC, and SOC via affecting plant growth and associated above- and belowground litter input, but decreased soil fungal and bacterial diversity via its negative effect on soil pH (Figure 7). In addition, the changes in bacterial and fungal diversity were negatively associated with SOC, with the standardized coefficient for soil fungal diversity (−0.59, p < .01) more than 1.5 times higher than that for bacterial diversity (−0.41, p < .01).

4 | DISCUSSION

Microbial diversity plays a vital role in soil C cycling as microbes control soil biochemical processes (Harris et al., 2021; Keller et al., 2021; Qin et al., 2021; Ye et al., 2018), and microbial diversity and soil C content are often coupled (Delgado-Baquerizo et al., 2013; Liu et al., 2014). However, in this meta-analysis, we found that soil microbial diversity is strongly negatively related to soil C content (mainly SOC, MBC, and DOC), and their correlation coefficients decreased with increasing N fertilization rate and experimental duration, suggesting that the linkage between microbial diversity and soil C is weakened by N fertilization rate and duration. This global meta-analysis presents evidence that long-term N fertilization led to the decoupling between microbial diversity and soil C.

4.1 | Nitrogen fertilization increased soil C content

The N limitation of primary production is well documented, and N availability can also limit soil microbial activity (Dai et al., 2018; Wang, Lu, et al., 2018). If soil microbial activity is limited by soil

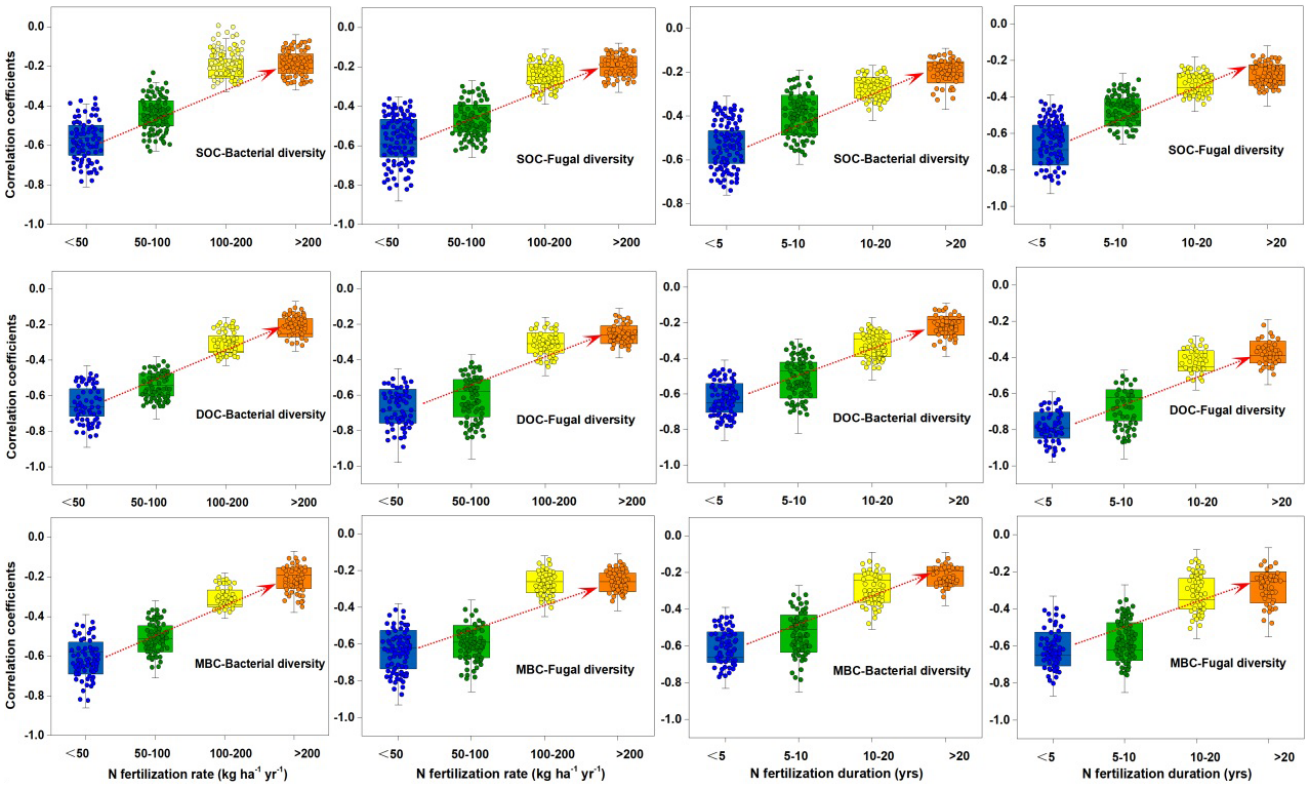

FIGURE 6 Dependence of the correlation coefficients between microbial diversity and soil organic carbon (SOC), microbial biomass carbon (MBC), or dissolved organic carbon (DOC) with N fertilization rate and duration. The lower and upper boundaries of the box represent the first and third quartiles, and the horizontal line represents the mean; the lower and upper bars reflect the 10th and 90th percentiles, respectively. Both N fertilization rate and duration effects have $p < .05$. [Colour figure can be viewed at wileyonlinelibrary.com]

N availability, N fertilization could decrease the rate of organic C decomposition, leading to increased soil C content (Buchkowski et al., 2017; Pendall, 2018; Tripathi et al., 2018; Zhalnina et al., 2015). Increased N availability should increase plant productivity and increase soil C content. Several experimental studies and meta-analyses show that increased aboveground C input to soil can enhance SOC storage (Chen et al., 2022; Deng et al., 2019; Jiang et al., 2021; Li et al., 2018; Liu & Greaver, 2010; Lu, Hou, et al., 2021; Lu, Vitousek, et al., 2021), as the aboveground plant C input is an important source of soil C (Lu et al., 2011; Lu, Hou, et al., 2021; Lu, Vitousek, et al., 2021; Niu et al., 2016). Plant root C is another crucial source of soil C and it forms stable soil organic matter much more efficiently than aboveground C (Feng et al., 2017; Xia & Wan, 2008; Zhang et al., 2018). Here, the positive relationship between root biomass and SOC provides further support for this linkage (Figure S3); plant biomass (including AGB, litter mass, and root biomass) is increased by N fertilization (Figure 2), suggesting that the contribution of plant C input to SOC is increased by N fertilization. In addition, the N effect on SOC first increased and then decreased with N fertilization rate and experimental duration (Figure 3), indicating that the effects of N fertilization on SOC can be temporally variable under N fertilization. In many experiments, SOC has been found to increase at lower N fertilization near 20 kg ha^{-1} year^{-1} (Cheng et al., 2018; Eastman et al., 2021; Li & Chang, 2015).The negative N fertilization effect on SOC is only visible at a high N fertilization rate (Paustian et al., 1992). Our global meta-analysis shows that the largest effect size of N fertilization on SOC was achieved when the N fertilization rate was 100 kg ha^{-1} year^{-1} and the fertilization duration was 10 years (Figure 4), suggesting that intermediate N fertilization rate and duration were the most effective in increasing SOC.

Previous meta-analyses found that microbial biomass declined by 6%–15% under N fertilization (Dai et al., 2018; Treseder, 2008; Zhang et al., 2018). Although N fertilization could increase resource availability that may stimulate microbial growth, it also might induce soil acidification that may inhibit microbial growth (Li et al., 2018; Niu et al., 2016; Wang, Lu, et al., 2018). However, the results are inconsistent among different forest ecosystems, with positive (Li et al., 2016), negligible (Zhang, Shen, et al., 2015), and negative effects of N fertilization (Van Der Heijden et al., 2008). Here, we found that MBC was increased by N fertilization as N fertilization increased litter and root biomass input (Figure 2). The effects of N fertilization on MBC are often dependent on the amount of N added and the experimental duration (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Li, Wang, et al., 2020; Li, Zeng, et al., 2020; Van Der Heijden et al., 2008), with positive effects of N fertilization on MBC occurring when N fertilization rate was less than 100 kg ha^{-1} year^{-1} and experimental duration was less than 10 years (Zhang et al., 2018).

The higher SOC leads to a greater production of DOC (Guo et al., 2020). Nitrogen fertilization increased litter decomposition, as well as root production, resulting in higher DOC input from plant

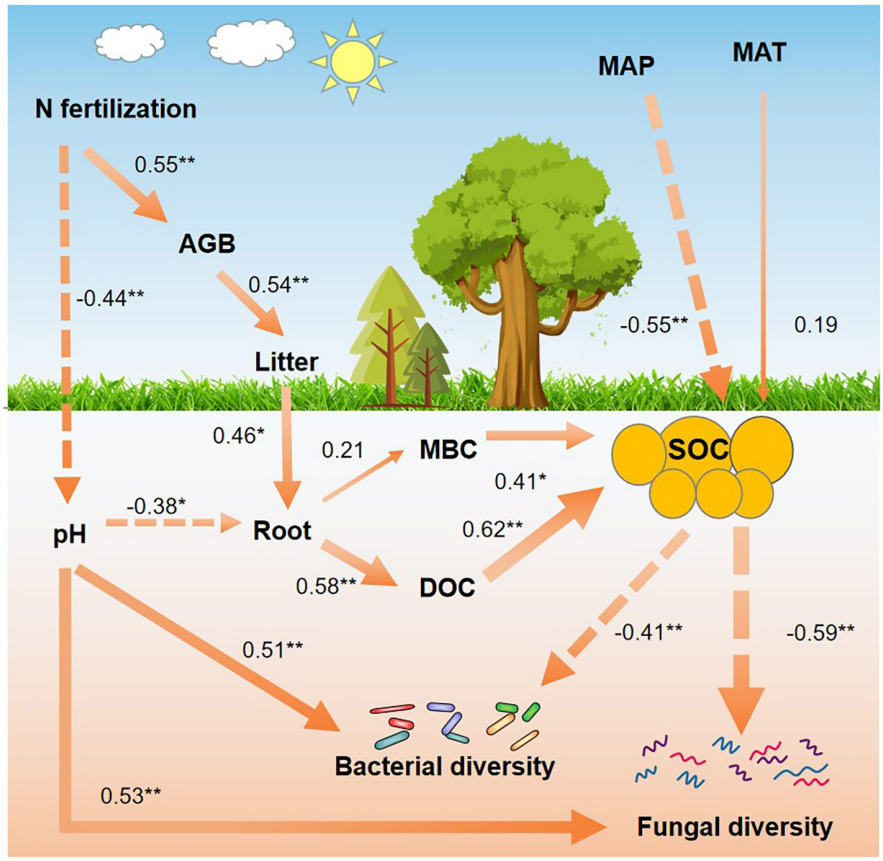

FIGURE 7 Structural equation modeling (SEM) depicting the multiple relations of microbial diversity with environmental factors at the global scale, and the values are the standardized path coefficients from model. The solid orange lines are the positive relationships and the dash orange lines are the negative relationships, respectively. Arrows represent a directional influence of one variable upon another. The numbers beside the arrows are standardized path coefficients. The thickness of the arrows is proportional to the magnitude of the standardized path coefficients. R^2 stands for the amount of variation interpreted by variables, which is calculated after 999 bootstraps, and the significant level is set at $^{*}p < .05$, $^{**}p < 0.01$. AGB, aboveground biomass; DOC, dissolved organic carbon; MAP, mean annual precipitation; MAT, mean annual temperature; MBC, soil microbial biomass carbon; SOC, soil organic carbon; STN, soil total nitrogen. [Colour figure can be viewed at wileyonlinelibrary.com]

residues (Liang et al., 2017; Wang, Liu, & Bai, 2018). In previous studies, increases in plant biomass were significantly higher with urea (organic) than with NH_4-N and NO_3-N (inorganic), leading to a greater input of plant residue into soil with urea, and the increasing plant residue enhances C input into soil (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Li, Wang, et al., 2020; Li, Zeng, et al., 2020; Peay et al., 2016; Van Der Heijden et al., 2008; Wagg et al., 2014). This explains why SOC, MBC, and DOC were significantly higher with organic N fertilization compared to inorganic N fertilization in our meta-analysis (Figure 3).

4.2 | Nitrogen fertilization decreased soil microbial diversity

Since N is a limiting nutrient in most terrestrial ecosystems, N fertilization may increase microbial activities by eliminating the N limitation (Deng, Hui, et al., 2017; Deng, Shangguan, et al., 2017; Peay et al., 2016; Wagg et al., 2014). While increased N fertilization rate could relieve N limitation in some ecosystems (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Dai et al., 2018; Yang et al., 2018; Zhang et al., 2018), we found that the responses of bacterial and fungal diversity decreased with increasing N fertilization rate and experimental duration, depending on ecosystem type (Figure 3). Soil microbes in grasslands are often constrained by C and moisture limitations. Previous studies suggested that soil moisture limitation may decrease the stability and diversity of microbial populations (Figure 2; Smith et al., 2021). Nitrogen fertilization might aggravate the water limitation by promoting plant growth, which in turn, can decrease soil microbial substrate availability and limit microbial growth and population size (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Li, Wang, et al., 2020; Li, Zeng, et al., 2020). Low soil water availability may favor soil microbes that tolerate dry environments to survive, but eliminate species that are not resistant to drought. In addition, nutrients may become more limited by drought in grasslands and indirectly affect microbial diversity (Li et al., 2018; Niu et al., 2016; Wang, Lu, et al., 2018; Yang et al., 2021).

In most temperate forests, increased N availability may reduce the need for plants to invest C to the belowground system for nutrient acquisition, resulting in a shift in C allocation to aboveground tissue production at the expense of root production (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Li, Wang, et al., 2020; Li, Zeng, et al., 2020; Treseder, 2008). As a result, increased N availability and the associated decrease in pH may result in decreased root biomass and root exudation, decreasing microbial diversity (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021). However, we found that N fertilization increased microbial diversity in temperate forests (Figure 3). It is possible that N fertilization could mitigate the temperature limitation in temperate forests (Liu et al., 2020), leading to the positive effect of N fertilization on soil microbial diversity. In global agroecosystems, the Shannon diversity index was decreased by 4.5% by mineral N addition and by 11.8% by straw N addition (Dang et al., 2022). Our results (Figure 3) also show that N fertilization increased soil N availability, microbial connectivity and dispersal, and anaerobic niches, resulting in an increase

in anaerobic taxa and a decrease in diversity in croplands (Dang et al., 2022).

4.3 | Factors driving soil C and microbial diversity under N fertilization

The negative relationships between soil microbial diversity and AGB, root biomass, and the positive relationship among DOC, SOC, and AGB, litter mass, root biomass (Figure S3) support that N fertilization enhances plant biomass and litter mass, exudate C incorporation into soil, and then, SOC and DOC accumulation (Dai et al., 2018; Wang, Lu, et al., 2018; Wu et al., 2021; Yang et al., 2017; Zhang et al., 2018). Moreover, MBC was positively correlated with SOC and AGB (Figure S3), suggesting that N fertilization affected SOC mainly through driving C input.

The N fertilization effect on soil microbial diversity (Figure 7) is consistent with Cassman et al. (2016) and Yang et al. (2021), as N fertilization significantly decreased microbial diversity via decreasing soil pH, causing toxic elements to accumulate in soils under high rates of N fertilization (Liu & Greaver, 2010; Romero-Olivares et al., 2017; Zhang, Liu, et al., 2015). Low soil pH increases the mortality of soil microbes and/or plant roots, and the release of DOC and MBC, benefiting the accumulation of SOC (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Xu, Li, et al., 2021; Xu, Xu, et al., 2021), and thus, soil pH was negatively correlated with DOC and SOC (Figure 7). Moreover, we found that SOC significantly decreased with MAP (Figure 7), suggesting that soil water availability plays a crucial role in affecting soil C dynamics (Bahram et al., 2018; Buchkowski et al., 2017; Delgado-Baquerizo et al., 2018; Pendall, 2018). Additionally, the standardized path coefficients of soil pH explaining for fungal diversity were higher than those for soil bacterial diversity (Figure 7), demonstrating the greater sensitivity of soil fungal diversity to global N fertilization than soil bacterial diversity (Fang et al., 2018; Field & Pressel, 2018; Lundberg & Teixeira, 2018; Tripathi et al., 2018; Yang et al., 2020, 2021; Zhang et al., 2018). Soil fungi are more sensitive to the decomposition of SOC and even soil C cycling than soil bacteria (Lu et al., 2011; Zhalnina et al., 2015), and thus, fungal diversity was more sensitive to N fertilization, if the latter had a positive effect on SOC (Tripathi et al., 2018; Yang et al., 2017; Zhalnina et al., 2015). Soil fungi are adapted to a greater range of soil pH due to their thick and interconnected chitin cell walls (Fierer & Jackson, 2006; Li et al., 2018; Wang, Lu, et al., 2018; Zhang et al., 2018). This would cause the higher microbial C assimilation efficiency of fungi under N fertilization (Fang et al., 2018; Field & Pressel, 2018; Geml & Wagner, 2018).

4.4 | Linkage between soil microbial diversity and soil C under N fertilization

The gradually increased response ratios of SOC, MBC, DOC, but decreased response ratios of microbial diversity with N fertilization rate and experimental duration result in the strongly negative linear relationships between microbial diversity and SOC, MBC, and DOC (Figure 5). This means that soil C and microbial diversity were decoupled; however, the absolute values of these correlation coefficients gradually decreased with N fertilization rate and duration (Figure 6), suggesting that the negative relationships between soil C and microbial diversity were weakened by increasing N fertilization rate and duration. In addition, MBC and DOC were positively related to SOC (Figure S3); however, these relationships were decreased by N fertilization rate and duration (Figure S4), suggesting that positive correlations among SOC, MBC, and DOC were also weakened by the increasing N fertilization rate and duration.

In a simple conceptual model (Figure 8), N fertilization can stimulate plant biomass production by relieving N limitation (Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Delgado-Baquerizo, Giaramida, et al., 2016; Delgado-Baquerizo, Maestre, et al., 2016; Lundberg & Teixeira, 2018; Xu, Li, et al., 2021; Xu, Xu, et al., 2021; Zhou et al., 2017); however, the magnitude of this stimulation can change over time, owing to the degree of co-limitation by other resources [e.g., phosphorus (P), potassium (K), micronutrients, light, and water] (Cardinale et al., 2012; Li, Wang, et al., 2020; Li, Zeng, et al., 2020; Niu et al., 2016; Yu et al., 2019). Therefore, microbial diversity and soil C responses to N fertilization in terrestrial ecosystems can be temporally dynamic and nonlinear (Chen et al., 2019; Chen, Chen, et al., 2021; Chen, Hu, et al., 2021; Zhang et al., 2018). However, N saturation occurs when supplies of N are in excess of the total combined plant and microbial demand, and thus, N saturation alleviates N limitation for soil C content and microbial diversity (Niu et al., 2016; Philippot et al., 2013; Singh et al., 2010; Zhang et al., 2018). Here, our results showed that SOC, MBC, and DOC decreased with soil microbial diversity across different ecosystems, with more pronounced negative associations under increasing N fertilization rate and experimental duration (Figure 4). Also, correlations between soil microbial diversity and SOC, MBC, and DOC were attenuated by high N fertilization rate and long experimental duration (Figure 6). These findings revealed that the linkage between microbial diversity and soil C was weakened by N fertilization in terrestrial ecosystems, which has implications for understanding soil C cycling under global change.

Previous studies showed that loss of microbial diversity will likely reduce ecosystem multifunctionality (Chen et al., 2020; Delgado-Baquerizo et al., 2020; Qiao et al., 2022). The redundancy of microbial species and functions means that a reduction in any group of microbial species may have little effect on overall soil function (Bastida et al., 2021; Wang, Lu, et al., 2018). For example, Gram-positive bacteria likely play an important role in the C acquisition by microbial communities and the decomposition of SOC, especially when the fungal biomass decreased under external N input (Zhu et al., 2022). Here, the loss in microbial diversity from N fertilization was decoupled with the increase in SOC (Figure 3), suggesting that the ecosystem function to store SOC was being maintained.

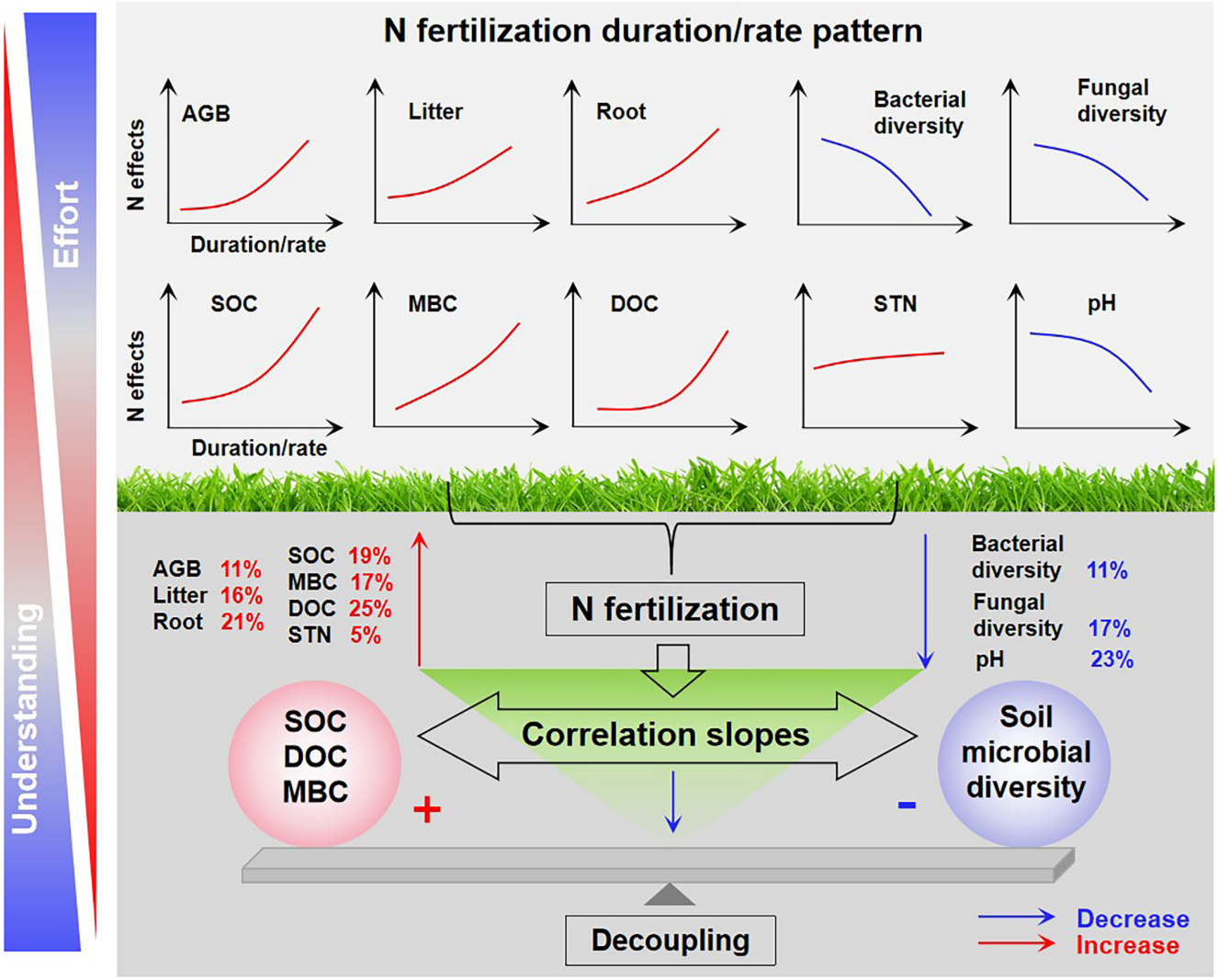

FIGURE 8 A simple conceptual model of the impacts of N fertilization on plant biomass, soil C, microbial diversity, and their temporal/ratio patterns. Red arrows represent positive N impacts/increasing plant and soil carbon responses, whereas blue arrows represent negative N impacts/decreasing microbial diversity responses. The relative contribution is shown next to the corresponding factor. The absolute value of correlation slopes between soil organic carbon (SOC), microbial biomass carbon (MBC), dissolved organic carbon (DOC), and soil microbial diversity decreased after N fertilization duration/rate. [Colour figure can be viewed at wileyonlinelibrary.com]

Our study has two important implications. First, the initial soil condition is an important factor that influences changes in soil C and microbial diversity under N fertilization. For example, if the soil C:N ratio is more than 10, N fertilization may mitigate the N limitation to microbes, and the negative effect of N fertilization on microbial diversity would not be severe; in contrast, when soil C:N ratio was less than 10, N fertilization would aggravate microbial N limitation, and enhance the negative N fertilization effect (Chen et al., 2013). Moreover, the negative effect of N fertilization on microbial diversity was greater in alkaline than in acidic soils. Therefore, when studying the effect of N fertilization, the initial environmental condition should be fully considered. Second, several modeling efforts have confirmed that the incorporation of microbial diversity into soil C models can substantially improve the projection of both the direction and magnitude of C–climate feedback (Delgado-Baquerizo et al., 2017; Delgado-Baquerizo, Giaramida, et al., 2016; Perveen et al., 2014). Our results of soil C and microbial diversity to N fertilization identified here support the utility of explicitly incorporating microbial diversity information into models for predicting changes of soil C under different global change scenarios.

Finally, existing literature usually reports certain stage of the experiment rather than monitoring soil C and microbial diversity continuously. This could lead to a potential bias in the understanding and prediction of the soil C dynamics as contrasting conclusions might be drawn from short- and long-term studies. In addition, N fertilization rate in existing studies are often far exceeding the natural N deposition rate (Delgado-Baquerizo et al., 2020; Domeignoz-Horta et al., 2020). These high levels of N inputs might bias our ability to understand and predict the effects of actual N deposition on soil C cycling microbial diversity. Therefore, long-term continuous observations are imperative for a comprehensive understanding of soil C and microbial diversity responses to N fertilization.

5 | CONCLUSIONS

We conclude that soil microbial diversity was strongly negatively related to SOC, MBC, and DOC, and the relationships were weakened with increasing N fertilization rate and experimental duration. Although N fertilization rates within the range of 50–100 kg ha^{-1} year^{-1} could be regarded as the threshold for maintaining SOC, MBC, DOC, and microbial diversity, simulated N fertilization trials are often carried out at higher rates, making the N fertilization effects on microbial diversity–soil organic C relationships variable and interpretation of the results difficult. Long-term N fertilization experiments covering a range of N application rates help improve our understanding of the N effect on soil C and microbial processes. Understanding the effect of long-term N fertilization on the linkages between soil C cycling and microbial processes is essential for managing ecosystem processes.

AUTHOR CONTRIBUTIONS

Yang Yang and Shaoshan An conceived and designed this meta-analysis. Yang Yang, Liangxu Liu, Ting Li, Yanxing Dou, and Jiangbo Qiao co-collected data. Yang Yang and Shaoshan An drafted the original manuscript. Yunqiang Wang, Xinli Chen, and Scott X. Chang provided very constructive suggestions. Scott X. Chang rewrote part of the manuscript.

ACKNOWLEDGMENTS

This study was funded by the Strategic Priority Research Program of Chinese Academy of Science (No. XDB40020203), the National Natural Sciences Foundation of China (42107282), the Natural Science Foundation of Shanxi Province (2021JM-213), the Open Fund of State Key Laboratory of Loess and Quaternary Geology (SKLLQG1915), the Western light Foundation of the Chinese Academy of Sciences (No. XAB2019B11).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available at Dryad via https://doi.org/10.5061/dryad.7h44j0zxd.

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SUPPORTING INFORMATION

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How to cite this article: Yang, Y., Chen, X., Liu, L., Li, T., Dou, Y., Qiao, J., Wang, Y., An, S., & Chang, S. X. (2022). Nitrogen fertilization weakens the linkage between soil carbon and microbial diversity: A global meta-analysis. *Global Change Biology*, *28*, 6446–6461. https://doi.org/10.1111/gcb.16361