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Leguminous plants significantly increase soil nitrogen cycling across global climates and ecosystem types

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Abstract

Leguminous plants are an important component of terrestrial ecosystems and significantly increase soil nitrogen (N) cycling and availability, which affects productivity in most ecosystems. Clarifying whether the effects of legumes on N cycling vary with contrasting ecosystem types and climatic regions is crucial for understanding and predicting ecosystem processes, but these effects are currently unknown. By conducting a global meta-analysis, we revealed that legumes increased the soil net N mineralization rate (R_{min}) by 67%, which was greater than the recently reported increase associated with N deposition (25%). This effect was similar for tropical (53%) and temperate regions (81%) but was significantly greater in grasslands (151%) and forests (74%) than in croplands (−3%) and was greater in in situ incubation (101%) or short-term experiments (112%) than in laboratory incubation (55%) or long-term experiments (37%). Legumes significantly influenced the dependence of R_{min} on N fertilization and experimental factors. The R_{min} was significantly increased by N fertilization in the nonlegume soils, but not in the legume soils. In addition, the effects of mean annual temperature, soil nutrients and experimental duration on R_{min} were smaller in the legume soils than in the nonlegume soils. Collectively, our results highlighted the significant positive effects of legumes on soil N cycling, and indicated that the effects of legumes should be elucidated when addressing the response of soils to plants.

KEYWORDS
climatic regions, ecosystem types, experimental management, legumes, meta-analysis, net nitrogen mineralization

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1 | INTRODUCTION

Nitrogen (N) availability is the most important factor influencing many terrestrial ecosystems and their responses to global changes (Fernández-Martínez et al., 2014; Reich et al., 2006). Plants can have positive or negative effects on ecosystem N dynamics and availability by influencing N inputs or losses (Chen et al., 2021; Mueller et al., 2013). As an important component of terrestrial ecosystems and a source of proteins and nutrients for human and animal consumption, legumes are the most diverse and widespread group of plants with the capacity to fix N from the atmosphere (Foyer et al., 2016; Vitousek et al., 2013). For example, half of the N demand in agricultural systems is met by leguminous crops (Fowler et al., 2013), which mitigates the chemical N fertilizer inputs to soils and their negative environmental impacts (Drinkwater et al., 1998; Foyer et al., 2016). In addition, in comparison to nonleguminous species, leguminous plants have higher N concentrations and decomposition rates of litter, usually increasing soil N availability and facilitating a better environment for the growth of coexisting plants by increasing soil organic carbon (C), soil nutrients and humus content (Pirhofer-Walzl et al., 2012; Xu et al., 2020). In light of the combined the importance of legumes in affecting N cycling and of N cycling in regulating the feedback of ecosystems to global change factors, there is an urgent need to identify how legumes affect soil N cycling in the context of global change and agricultural demand.

As a key N cycling process that has been widely used to assess soil N availability and plant growth (Chen et al., 2021; Risch et al., 2019), soil N mineralization has been reported to be enhanced by legumes in various ecosystems by increasing substrate availability, alleviating microbial nutrient constraints and changing soil properties (Gei & Powers, 2013; Mueller et al., 2013; Wei et al., 2019). Given that these processes have been shown to differ significantly between managed (i.e., croplands) and unmanaged ecosystems (i.e., grasslands and forests; Elrys et al., 2021; Li et al., 2021), the effects of legumes on N cycling are likely dependent on ecosystem types. Generally, managed ecosystems experience extensive anthropogenic activities (e.g., fertilization), which may inhibit the effects of legumes on soil N cycling because of the downregulation of N fixation in N-rich environments (Liu et al., 2011; Menge et al., 2009). For example, Tamagno et al. (2018) found that N fertilizer reduced the peak of biological N fixation by up to 16% in applications at the full flowering stage of soybean at 23 sites across the US Midwest. In addition, the harvest of legume biomass in managed ecosystems may also reduce the effects of legumes. On the other hand, in unmanaged ecosystems, legumes play an important role in forcing N cycling (Batterman et al., 2013; Gei et al., 2018). Such ecosystems do not receive anthropogenic N fertilizers and are thus subject to strong N limitation (Du et al., 2020). Given that the growth and N fixation of legumes are stronger in the absence of management (Ma & Chen, 2021), their effects on N cycling should be stronger in unmanaged ecosystems than in managed ecosystems. In addition, the return of legume biomass as litter into soils in unmanaged ecosystems would increase the effects of legumes on N cycling due to the high N content of legume litter (Makkonen et al., 2012; Wang et al., 2010). Moreover, unmanaged ecosystems are usually affected by natural processes (e.g., fire and grazing), which have significant impacts on the succession of legume communities and thus on the growth and N fixation of legumes (Houseman et al., 2020; Tierney et al., 2019). Nevertheless, such a hypothesis regarding how legumes impact N cycling in contrasting ecosystem types is not examined at the global scale.

In addition, the growth and N fixation ability of legumes are significantly affected by climate (Liao et al., 2017; Menge et al., 2014). N fixation allows legumes to maintain high foliar N concentrations; thus, they use water more efficiently than nonlegumes (Adams et al., 2016), which may further regulate the effects of climate on the ecosystem because of the alteration in the supply and demand of both N and water in legumes and nonlegumes (Pellegrini, 2016). For example, it has been shown that climate plays a greater role than fire frequency and biome type in determining the distribution of N-fixers across tropical savanna and forest biomes (Pellegrini et al., 2016). Similarly, warming has been shown to increase the growth of legumes in a long-term grassland experiment in Minnesota (Cowles et al., 2016). Moreover, warming increases N fixation at the middle and high latitudes but reduces N fixation in low-latitude tropical regions in analyses based on a theoretical framework that considers interactions of C and nutrients to estimate rates of terrestrial N fixation (Wang & Houlton, 2009). In addition, drought can restrict legume growth through lowered stomatal conductance and metabolic processes and can limit N fixation directly by decreasing root nodule function (Dovrat et al., 2018; Serraj, 2003). Legumes preferentially support N fixation on root sections under conditions of ample water relative to root sections of the same plant grown under dry conditions (Marino et al., 2007), suggesting downregulation of N fixation under drought (Dovrat et al., 2018; Wurzburger & Miniat, 2014), even if the growth of legumes is less affected than that of nonlegumes under drought conditions (Pellegrini et al., 2016). For instance, drought has been shown to reduce nodule biomass and nitrogenase activity (33% and 27%, respectively) in eight species of neotropical woody legumes in a greenhouse experiment (McCulloch et al., 2021). This current knowledge highlights the highly complex and interwoven effects of legumes, biomes and climate on terrestrial N cycling. Addressing such complex effects is a crucial step toward better understanding terrestrial biogeochemical cycling and is essential for ecosystem N management. However, it is difficult to quantitatively understand such complex effects based on studies conducted within a single ecosystem or at a small scale and requires analysis based on a global dataset across different climatic regions and ecosystem types.

Herein, to address how the effects of legumes vary with ecosystem types, climatic regions and experimental management, we conducted a global examination on the effects of legumes on the soil net N mineralization rate (R_{min}) based on a meta-analysis with 406 observations from 97 publications. We aimed to answer the following questions: (1) How do the effects of legumes on R_{min} vary with ecosystem types, climatic regions and experimental management as

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these factors significantly affect the growth and N fixation of legumes (Liao et al., 2017; Menge et al., 2014)? (2) How do the relationships between N cycling and their driving factors (climate, experimental management, soil properties) vary between legume and nonlegume systems because both ecosystems have contrasting N limitations? The duration of the experiment can significantly influence the growth and N fixation of legumes in the community (Eisenhauer et al., 2011; Mueller et al., 2013) and thus influence the effects of legumes on N cycling. In addition, researchers may use various approaches to determine N cycling (Robertson et al., 1999). We therefore included the duration of the experiment and the method for measuring N mineralization as aspects of experimental management to examine their influence on legume effects. Our global dataset includes paired legume treatments (i.e., legumes vs. nonlegumes), ecosystem types (croplands, forests and grasslands), climatic regions (tropical and temperate regions), durations of experiments (short- vs. long-term experiments) and methods of R_{min} measurement (in situ vs. laboratory incubation methods). Some important soil properties, including soil pH, soil organic C, total N, nitrate N, ammonium N, available phosphorus, soil moisture, microbial biomass C and microbial biomass N, were also collected. This allowed us to conduct various comparisons and analyses to answer the above scientific questions. Overall, our meta-analysis sought to capture the effects of legumes on N cycling across various climatic regions and ecosystem types to advance our current understanding of soil N cycling based on plant functional groups.

2 | MATERIALS AND METHODS

2.1 | The global dataset

Our global dataset was collected by searching published peer-reviewed articles using the Web of Science (http://apps.webofknowledge.com) and the China National Knowledge Infrastructure Database (http://www.cnki.net/). We screened articles using the keywords “legume” or “N-fixing species” or “land use” AND “soil N mineralization” or “soil N cycling” or “soil N transformation” or “soil N availability.” The following criteria were applied in selecting the studies. (1) Legume and nonlegume (control) plots were compared within the same independent experiment, and the experiments were conducted under the same climate, soil and management conditions to avoid confounding noise. (2) Target variables were estimated by utilizing topsoil samples (mostly within a depth of 10 cm). (3) The details of the experimental conditions (i.e., temperature, moisture, and incubation period) for measuring the net N mineralization rate (R_{min}), nitrification rate (R_{nit}), and ammonification rate (R_{amm}) were explicitly described in the original articles. (4) The means, standard deviation (SD), and sample size (n) of the target variables were reported in the text or could be calculated from the reported data, and the standard error (SE) was converted to SD using the following equation: $\text{SD}=\text{SE}\times\sqrt{n}$. (5) If multiple independent experiments conducted under different environmental conditions or ecosystem types were reported in the same article, each experiment was considered an independent data record. (6) For studies with multiple factors being manipulated (e.g., plant species richness and elevated CO_2), we only extracted data from legume and nonlegume treatments of control treatments. (7) For forest ecosystems, the data from the organic soil layer were excluded because of the significant variations in soil properties between organic soils and mineral soils, which would prevent comparisons among ecosystem types. The review and search of the dataset was conducted by following the preferred reporting items for meta-analysis (PRISMA) guidelines (Moher et al., 2009; Figure S1). Finally, 406 records from 97 articles were selected for the meta-analysis (Figure 1 and Notes S1).

When the functional groups of the plants (i.e., legume vs. nonlegume) were clearly provided in the article, we directly extracted the data that met the criteria. Otherwise, we queried the characteristics of the plants from the Royal Horticultural Society website (https://www.rhs.org.uk/). In addition, when studies included multiple species of either legumes or nonlegumes, we extracted multiple data points and averaged the data for legumes or nonlegumes, generating one effect size. For studies that included multiple plant functional groups (i.e., C3 grasses, C4 grasses, forbs, legumes), we used legumes as a treatment and the other functional groups as controls to generate multiple effect sizes.

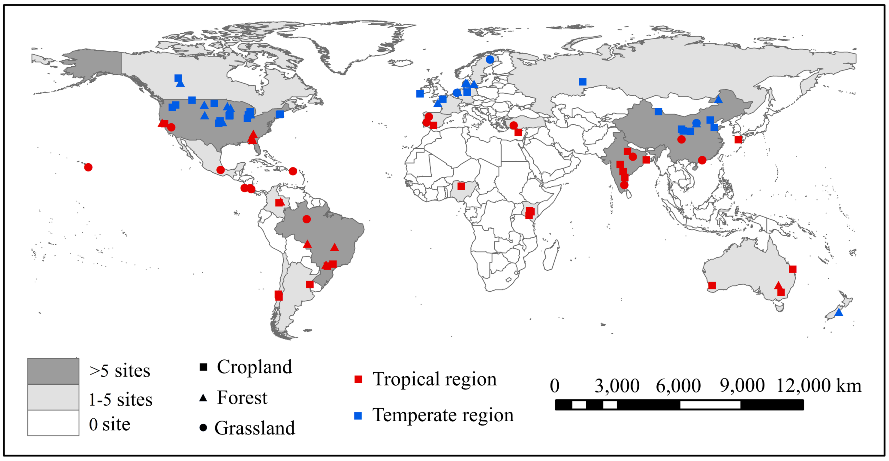

FIGURE 1 Global distribution of study sites included in this meta-analysis. Graded colors illustrate the number of experimental sites per country. All sites are grouped to three ecosystem types (croplands, forests and grasslands) and two climatic regions (tropical and temperate regions). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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In our dataset, manipulations of legume and nonlegume plots varied with ecosystem types. In croplands, legume and nonlegume crops were usually planted each year and harvested during the harvest season. In grasslands and forests, legume plants were planted (98.2% of observations in our dataset) or naturally existed (1.8%) in the legume plots, while legume plants were naturally absent (8.9%) or nonlegume plants were planted (91.1%) in the nonlegume plots. The plots from which legumes were manually removed to create control treatments were not included in our dataset for the three ecosystem types. Therefore, in our dataset, both the legume and nonlegume plots that were included had similar initial conditions, which allowed us to examine the effects of legumes by comparing legume and nonlegume plots. In our dataset, only a few articles (11.8%) provided information on legume density (number of legumes in the community), so we did not include it as a factor in our statistical models.

For each independent experiment, R_{min}, R_{amm} and R_{nit} were extracted from the legume and nonlegume (control) treatments. For studies that reported mineralization rates at various incubation times ($n=36$), we extracted the results for approximately 1 month of incubation because most samples were incubated for this amount of time. For the studies that only reported one-time incubation results ($n=333$), we directly extracted those results. Some important soil properties, including soil pH, soil organic carbon (SOC), total N (TN), nitrate N (NO_3^-), ammonium N (NH_4^+), available phosphorus (AP), soil moisture (SM), microbial biomass carbon (MBC) and microbial biomass N (MBN), were also collected. In addition to soil properties, site information, which included latitude (with a range from 43.63°S to 66.52°N), longitude (155.25°W to 172.50°E), mean annual temperature (MAT, −6.2 to 27.9°C), and mean annual precipitation (MAP, 72 to 4600 mm), was obtained to the extent possible from the original articles, from relevant studies or from the climatic database (https://power.larc.nasa.gov/data-access-viewer/). For studies that lacked climate data, we derived MAT and MAP from the WorldClim Database based on latitude and longitude (Fick & Hijmans, 2017). For the experiments that included N fertilizer (or N deposition), the rate of N fertilizer was included in the dataset.

The net N mineralization collected in our global dataset was measured using either laboratory ($n=160$) or in situ measurements ($n=209$). The laboratory measurements were taken from soils incubated under standard moisture and temperature conditions. The soils used in the laboratory measurements were collected from field experimental plots (mostly within a depth of 10 cm). The in situ measurements were collected using an undisturbed capped buried core method (mostly within a depth of 10 cm in our dataset; Risch et al., 2020; Robertson et al., 1999). The concentrations of NO_3^- and NH_4^+ in the soils at the beginning and end of either laboratory or in situ incubation were analyzed to calculate the metrics for net N mineralization. For soil N cycling metrics, we examined whether the effects of legumes varied with measuring conditions (i.e., incubation temperature, moisture and time) using a linear mixed-effect model with measuring conditions as fixed factors and the "study" as a random factor. Our results showed that the effects of legumes on N cycling metrics were not affected by measuring conditions (Table S1); thus, these factors could be neglected in our comparison between legumes and nonlegumes.

To examine whether the effects of legumes varied with ecosystem types, climatic regions, and experimental factors, we grouped the dataset according to ecosystem types, climatic regions, experimental durations and methods of N mineralization measurements. The ecosystem types were grouped into croplands, forests and grasslands. The climatic regions were grouped into tropical regions (i.e., tropical and subtropical regions) and temperate regions (i.e., temperate and boreal regions) according to the 2010 Global Ecological Zones mapping (https://data.apps.fao.org/). The experimental duration was categorized into short- (<5 years) and long-term experiments (≥5 years) because of imbalanced sampling numbers for each duration of experiment (Figure S2). Five years was used as the time threshold to group short- and long-term experiments because this was based on a large survey of long-term research in the fields of ecology and evolution (Kuebbing et al., 2018). The measurement method for net N mineralization was divided into laboratory incubation and in situ measurements. Our primary examinations on the interactive influences among factors showed nonsignificant interactions on legume effects ($p>.05$), suggesting that the effects of such influencing factors were independent of each other. We therefore did not consider such interactive effects when examining legume effects within any subgroup.

2.2 | Meta-analysis

Since some N cycling metrics have negative values, this precluded the use of the response ratio (calculated as the natural log of the experimental mean over the control mean) as a metric for comparison between studies (Hedges et al., 1999). Here we utilized the standardized mean difference metric "Hedge's d" for analysis, which is less biased by small sample size (Hedges & Olkin, 1985). The effect size (d) and pooled standard deviation (S) were calculated as follows:

$$d=\frac{Xt-Xc}{S}\times\left(1-\frac{3}{4\times\left(n_t+n_c-2\right)-1}\right) \tag{1}$$

$$S=\sqrt{\frac{\left(n_t-1\right)\times St^2+\left(n_c-1\right)\times Sc^2}{n_t+n_c-2}} \tag{2}$$

where Xt and Xc are the values of a given variable in the treatment (legume) and control (nonlegume) groups, respectively. n_t and n_c the sample sizes and St and Sc the standard deviations of the treatment and control groups, respectively.

The interpretation of the standardized mean effect size differs from the response ratio, as the standardized mean effect size cannot be expressed as a percent change in response to an experimental treatment compared with a control. Rather, it represents how far removed the standardized mean of the experimental treatment is from the standardized mean of the control measured in standard deviation.

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The effect size was weighted using the inverse of the pooled variance (v) as follows:

$$v = \frac{n_c + n_t}{n_c \times n_t} + \frac{d^2}{2 \times (n_c + n_t)} \tag{3}$$

A weakness of meta-analyses is that experimental treatments (i.e., legumes) are compared with several controls (i.e., C3 grasses, C4 grasses and forbs) within a study. This artificially increases the number of replicate pairs and violates the assumption of independence. Therefore, to prevent overestimation of the precision of the mean effect size, the resulting pairs were combined into one composite effect size using the variance (v') as follows (Aguilera et al., 2013; Hungate et al., 2009):

$$v'\left(\frac{1}{m} \times \sum_{i=1}^{m} d_i\right) = \left(\frac{1}{m}\right)^2 \times \left(\sum_{i=1}^{m} V_i + \sum_{i \neq j}\left(r_{ij} \times \sqrt{V_i} \times \sqrt{V_j}\right)\right) \tag{4}$$

where m represents the number of correlated pairs, d_i and V_i the effect size and variance of pairs, respectively, and r the correlation coefficient, which is equal to 0.5 because all pairs shared a common treatment.

The weighted effect size (d_+) and its corresponding 95% confidence intervals (CIs) were calculated using METAWIN 2.1 software with a categorical random effect model. This method provides an inference about the average effect in the entire population from which the included studies are assumed to be a random selection (Viechtbauer, 2010), and thus does not include either random effect or fixed factor (Hedges & Vevea, 1998). The CIs were generated by bootstrapping (9999 iterations; Hedges & Olkin, 1985; Rosenberg et al., 2000). The effect of a response variable can be considered significant at $p < .05$ if the 95% CIs do not intersect at zero. To test whether the effects of legumes on soil N cycling metrics differed by subgroup, a between-group heterogeneity (Q_B) test was performed. A significant Q_B indicates that the metrics are significantly different among subgroups (Rosenberg et al., 2000).

There is no rigorously applied framework for the interpretation of standardized means in terms of "effect sizes" because, unlike response ratios, they are probabilistic. That is, they describe the probability that a sample drawn from the control treatments would fall between the experimental mean and the control mean, assuming a normal distribution. By convention, for variables that do not overlap with Hedge's d of zero, a d value higher than 0.8 indicates a large effect, a d value of 0.2–0.8 shows a moderate effect and a d value of 0.0–0.2 displays a small effect (Hedges et al., 1999; Jeffery et al., 2016). A key point is that, using Hedge's d metric, an effect size of a variable analysis does not equate to the effect size of others in the independent analyses presented in this study. Only categories within individual analyses can be compared on a relative basis.

Publication bias may influence our meta-analysis results. We assessed the publication bias for each response metric by Spearman's rank correlating effect sizes and their variations (Rosenberg et al., 2000). We found that there was no publication bias for the metrics except for $R_{\min}$ and NO_3^- (Spearman $p = .04$ for $R_{\min}$ and $p = .01$ for NO_3^-; Table S2). We examined whether publication bias influenced our meta-analysis results by estimating the fail-safe number (Nfs) of $R_{\min}$ and NO_3^- (Orwin, 1983). The result from meta-analysis is assumed to be stable (or not influenced by publication bias) when the ratio of Nfs to ($5n + 10$) is greater than 1, where n is the sampling size (Jeffery et al., 2016; Zhao et al., 2022). In our analysis, the ratios were 4.73 and 2.57 for $R_{\min}$ and NO_3^-, respectively. Therefore, we did not consider publication bias in our analysis.

2.3 | Structural equation modeling

We constructed the conceptual framework of structural equation models (SEMs) on the basis of the bivariate relationships between $R_{\min}$ change and N fertilization and environmental factors (Figure S3). The SEMs require a relatively small sampling size (10 times the number of paths; Grace, 2006) and have been used in many studies with sampling sizes of 25–69 (Feng et al., 2022; Lu et al., 2022; Vieira et al., 2020). Hence, this approach can provide robust results with a relatively small sample group size and was appropriate for our study. All variables included in the SEMs were continuous. The climatic factors used in the above analysis were MAT and MAP for the experimental sites. The first axis of the principal component analysis (PCA) represents changes in soil nutrients based on SOC, TN, NO_3^-, and NH_4^+. PCA was conducted using the "FactoMineR" and "factoextra" packages in R software (version 4.2.1). In SEMs, the fixed variables were the environmental factors and the random variable was the "study." Shipley's d-separation test was used to examine whether any paths were missing from the model, and $p > .05$ indicated that no paths were missing and that the model was a good fit (Shipley, 2009, 2013). We reported the standardized coefficient for each path from each component model, and Fisher's C statistic and AIC values of the overall model by using the piecewiseSEM package (https://github.com/jslefche/piecewiseSEM) in R software (version 4.2.1). Moreover, to examine the relative importance of factors influencing $R_{\min}$ in systems with and without legumes, we independently ran two SEMs by using the same procedure as above. All figures showing d_+ values were plotted in OriginPro 2018 (OriginLab Corp.).

3 | RESULTS

3.1 | Overall effects of legumes on soil net nitrogen mineralization and soil properties

As expected, our meta-analysis showed that legumes increased the soil N cycling rate across the global dataset. On average, the $R_{\min}$, R_{nit} and R_{amm} in soils with legumes were higher than those in soils without legumes ($d_+ = 0.97$, 0.95 and 0.07, respectively; Figure 2).

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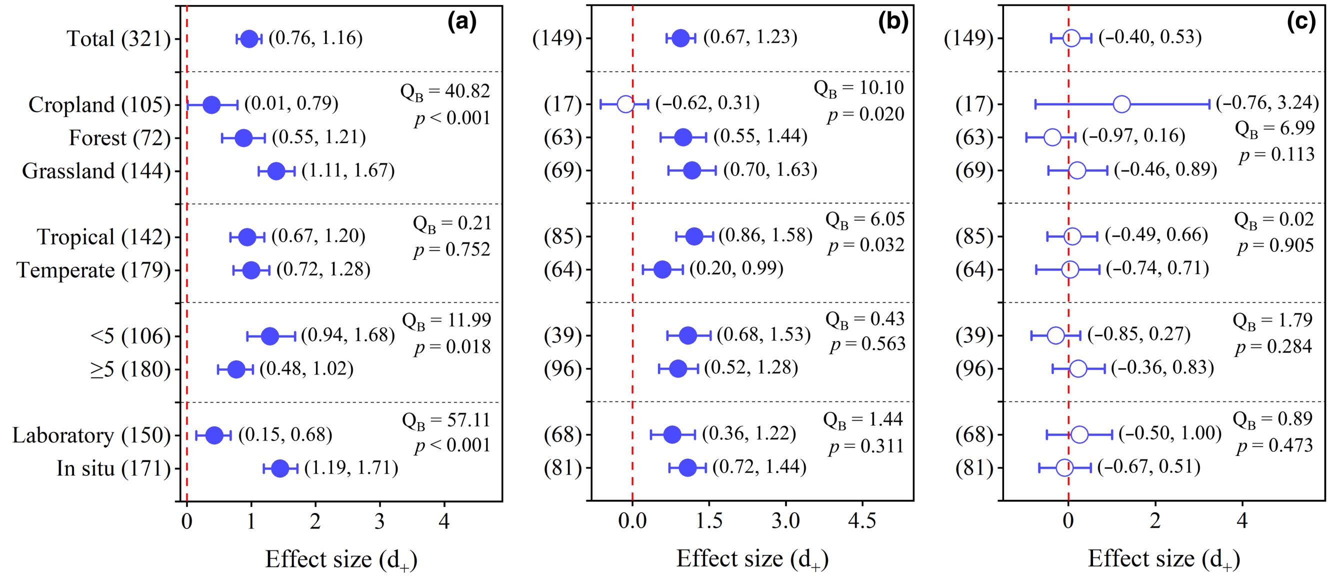

FIGURE 2 Effects of legumes on the rates of soil net N mineralization (R_{min}, a), net nitrification (R_{nit}, b) and net ammonification (R_{amm}, c). All plots represent the weighted effect size of different variables with 95% confidence intervals (CIs). The observation of each variable is displayed beside each bar in parentheses. If the 95% CIs do not overlap with zero the effect is significant at $p < .05$ (filled circles), otherwise the effect is not significant ($p > .05$; open circles). Q_B represents the heterogeneity in effect among groups, and the significant value of Q_B indicates significant differences among groups ($p < .05$). The vertical dash line indicates effect size of 0.

Moreover, in comparison to soils without legumes, soils with legumes had significantly higher SOC ($d_+ = 0.46$), TN ($d_+ = 0.85$), NO_3^- ($d_+ = 1.10$) and NH_4^+ ($d_+ = 0.16$) values but similar values of other soil properties (Figure 3).

3.2 | Variations in legume effects with climatic regions, ecosystem types and experimental management

The effects of legumes on R_{min} and R_{nit} varied with ecosystem types, with significantly higher effect sizes in grasslands ($d_+ = 1.39$ and 1.17) and forests ($d_+ = 0.89$ and 0.99) than in croplands ($d_+ = 0.38$ and −0.13; $p < .001$ and $p = .020$; Figure 2a,b). However, the effect of legumes on R_{amm} was not influenced by ecosystem types, with effect sizes of 1.23, 0.21 and −0.36 for croplands, grasslands and forests, respectively ($p = .113$; Figure 2c).

The effects of legumes on most soil N cycling metrics were independent of climatic regions (Figure 2). Among the climatic regions examined, the effects on R_{min} and R_{amm} were not affected by climatic regions ($p = .752$ and .905; Figure 2a,c). However, the effect of legumes on R_{nit} was significantly higher in tropical regions ($d_+ = 1.21$) than in temperate regions ($d_+ = 0.59$; $p = .032$; Figure 2b).

The effect of legumes on R_{min} was greater in short-term experiments ($d_+ = 1.29$) than in long-term experiments ($d_+ = 0.77$; $p = .018$; Figure 2a). Moreover, the legume effect on R_{min} measured by in situ incubation ($d_+ = 1.45$) was significantly higher than that measured by laboratory incubation ($d_+ = 0.43$; $p < .001$; Figure 2a). However, the effects of legumes on R_{nit} and R_{amm} were not affected by experiment duration and measurement method (Figure 2b,c). Hence, the effects of legumes on soil N cycling were climate-, ecosystem- and experimental management dependent.

3.3 | Key factors influencing the effects of legumes on soil net nitrogen mineralization

Structural equation modeling showed that N fertilization and changes in soil nutrients had important regulatory effects on the response of R_{min} to legumes (Figure 4). The environmental factors examined in our SEM explained 33.0% of the total variation in legume effects. N fertilization significantly decreased the response of R_{min} to legumes. Changes in soil nutrients induced by legumes significantly altered MBC change, which had a negative effect on the response of R_{min} to legumes. However, climatic conditions (MAT and MAP) had no impact on the effect of legumes on R_{min}.

3.4 | Legumes shifted the dependence of soil net nitrogen mineralization on influencing factors

We independently examined the relative importance of factors influencing R_{min} in systems with and without legumes (Figure 5). The R_{min} was affected by N fertilization in soils from both the legume and nonlegume treatments, but the effect in the nonlegume treatments was greater than that in the legume treatments. In addition, climatic conditions (MAT and MAP) not only directly influenced R_{min}, but also indirectly affected R_{min} by altering MBC, and the effect of MAT was

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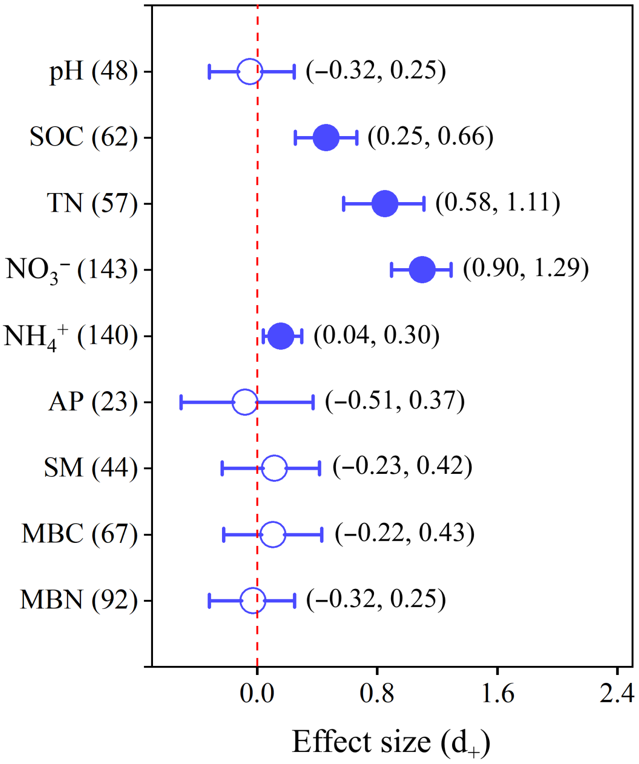

FIGURE 3 Effects of legumes on soil properties. The plot represents the weighted effect size of different variables with 95% confidence intervals (CIs). The observation of each variable is displayed beside each bar in parentheses. If the 95% CIs do not overlap with zero, then the effect is considered significant ($p < .05$; filled circles), otherwise the effect is not significant ($p > .05$; open circles). The vertical dash line indicates effect size of 0. SOC, soil organic carbon; TN, total nitrogen; NO_3^-, nitrate nitrogen; NH_4^+, ammonium nitrogen; AP, available phosphorus; SM, soil moisture; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen.

greater in nonlegume soils than in legume soils. Therefore, legumes significantly altered the dependence of R_{min} on N fertilization and environmental factors.

4 | DISCUSSION

In this study, we provide the first global assessment demonstrating that legumes significantly enhanced soil N cycling, and this effect was similar for tropical and temperate regions but was significantly greater in grasslands and forests than in croplands and greater in in situ incubation or short-term experiments than in laboratory incubation or long-term experiments. Moreover, N fertilization and changes in soil nutrients were the dominant factors that influenced the effects of legumes on R_{min}. The results from our study advance the current understanding of the effects of legumes on N cycling from the site scale to the global scale across ecosystem types and climatic regions.

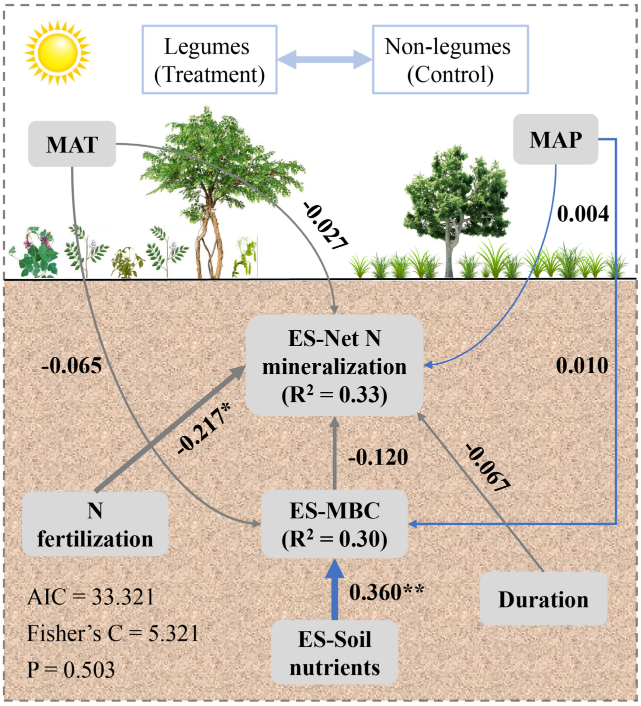

FIGURE 4 Piecewise structural equation model (SEM) assessing the direct and indirect effects of climatic factors (MAT and MAP), N fertilization, experimental duration, changes in soil nutrients (the first axis of the principal component analysis based on SOC, TN, NO_3^- and NH_4^+) and microbial biomass (MBC) on the response of net N mineralization to legumes. Numbers adjacent to arrows show standardized path coefficients. Blue and gray lines indicate positive and negative relationships, respectively, with the thickness representing the extent of influence. The R^2 values indicate the proportion of variance explained for each endogenous variable. ES, effect size; MAT, mean annual temperature; MAP, mean annual precipitation; MBC, microbial biomass carbon; Duration, experimental duration. Asterisks denote significant differences based on the Wilcoxon test. *$p < .05$ and **$p < .01$.

4.1 | Legumes increase the rate of nitrogen cycling worldwide

Our global analysis showed that legumes accelerated soil N cycling processes (Figure 2). We ascribed this result to the following three factors. First, organic materials (leaf litter, fine roots, and/or root nodules, C rhizodeposition) derived from legumes have high N content and provide many substrates for decomposers, which accelerates N mineralization because soil N cycling is dominated by microbes (Makkonen et al., 2012; Wang et al., 2010). Second, legumes decrease the soil C/N ratio due to the greater increase in N relative to C and increase soil moisture (Figure 3). Both low C/N ratios and high soil moisture stimulate microbial growth (Wendlandt et al., 2022), thus resulting in higher R_{min} in legume soils than in nonlegume soils. Third, the greater biomass of legumes leads to higher C input to soils than with nonlegumes (Yang et al., 2019), which accelerates N mineralization due to the priming effect (Gei

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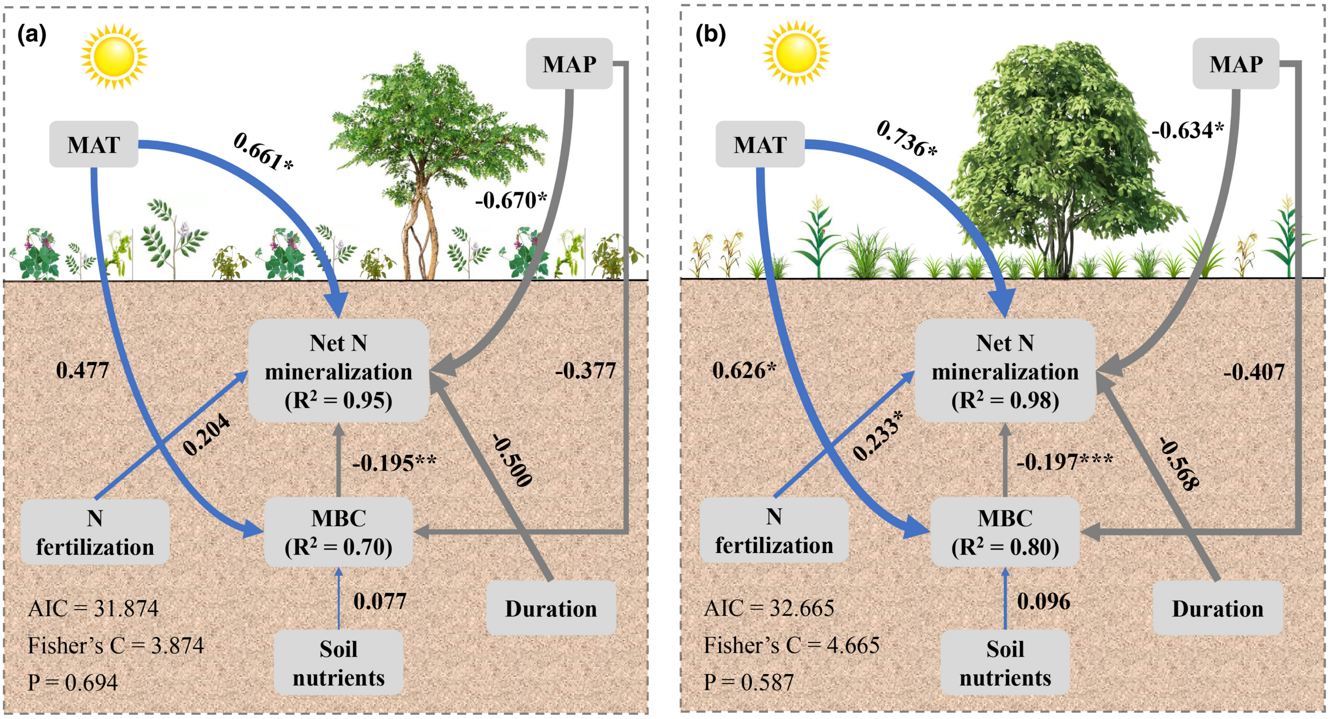

FIGURE 5 Piecewise structural equation model (SEM) assessing the direct and indirect effects of climatic factors (MAT and MAP), N fertilization, experimental duration, soil nutrients (the first axis of the principal component analysis based on SOC, TN, NO_3^- and NH_4^+) and microbial biomass (MBC) on soil net N mineralization in legume (a) and nonlegume (b) treatments. Numbers adjacent to arrows show standardized path coefficients. Blue and gray lines indicate positive and negative relationships, respectively, with the thickness representing the extent of influence. The R^2 values indicate the proportion of variance explained for each endogenous variable. MAT, mean annual temperature; MAP, mean annual precipitation; MBC, microbial biomass carbon; Duration, experimental duration. Asterisks denote significant differences based on the Wilcoxon test. $^*p < .05$, $^{**}p < .01$, and $^{***}p < .001$.

& Powers, 2013; Wei et al., 2019). This explanation is supported by the "microbial activation" hypothesis, which proposes that large amounts of C, N and other nutrients can be released in soils in a short span of time because of microbial activities caused by fresh C inputs (Kuzyakov et al., 2000).

It should be noted that the density of legumes in the community may have an important influence on the effects of legumes on N cycling (Rodriguez et al., 2020; Wei et al., 2019). However, because most of the articles only reported that their soil samples were collected or that N cycling was measured in legume plots but did not report the legume density in the legume plots, it is impossible for us to disentangle the influence of legume density from the effect of legume presence in our dataset. This may have led to uncertainties in our results. We hence recommend that the effect of legume density should be carefully quantified by manipulation experiments across multiple sites or by model prediction at the global scale.

4.2 | Variations in the effects of legumes with ecosystem types but not climatic regions

We found that the responses of R_{min} and R_{nit} to legumes varied with ecosystem types (Figure 2). The greater effects of legumes on soil N cycling in forests and grasslands were ascribed to the fact that the overall background N level (available N in soils from nonlegume plots) in forests and grasslands was significantly lower than that in croplands (Figure S4). Croplands receive not only atmospheric N deposition, but also chemical N fertilizers, while forests and grasslands receive only N deposition, and most of this deposited N is intercepted by the plant canopy, and only a small fraction enters the soil (Gaige et al., 2007; Guerrieri et al., 2015). Meanwhile, the effects of legumes on N fixation and soil N cycling were greater in soils with low N than in soils with high N (Mueller et al., 2013; Wei et al., 2019). In addition, this low background soil N level leads to a greater relative effect of legumes on soil NH_4^+ in forests and grasslands than in croplands (Figure S5a), which thus leads to higher R_{min} and R_{nit} given the significant contribution of R_{nit} to R_{min} (Raghurama & Sankaran, 2022; Yao et al., 2019). The significantly smaller effects of legumes in croplands were primarily because of the harvest of aboveground biomass and due to severe anthropogenic perturbations, such as tillage and fertilization. The removal of aboveground biomass significantly decreases C input to soils, which accelerates microbial C limitation and thus restricts N mineralization (O'Connell et al., 2015). In addition, ammonia oxidizers (i.e., oxidizing ammonium to nitrite) and the amoA gene that encodes ammonia monooxygenase (i.e., oxidizing ammonia to hydroxylamine) play critical roles in nitrification (Seeley et al., 2020), while legumes decrease the abundances of ammonia

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oxidizers and the amoA gene in agricultural systems (Paungfoo-Lonhienne et al., 2017; Yu et al., 2019) but not in forests (Rachid et al., 2013) and grasslands (Le Roux et al., 2013), which could also lead to a minimal effect on nitrification. Therefore, the positive effects of legumes on soil N cycling were greater in ecosystems with greater limitation by and competition for N.

We found that the effects of legumes on most soil N cycling metrics were not influenced by climatic regions (Figure 2), probably because of the contrasting impacts of MAP and MAT on legume effects (Figure 4). Generally, symbiotic N fixation by legumes is highly sensitive to water availability (Dovrat & Sheffer, 2019). A number of tropical and temperate legumes exhibit a reduction in N fixation when subjected to soil moisture deficiencies (Elli et al., 2022; Markham & Anderson, 2021; Rousk et al., 2017), mainly because nitrogenase activities rely on the quantity of carbohydrates supplied to nodules, and the supply decreases under water-limited conditions (Arfin-Khan et al., 2014). In addition, the limitations in legume growth induced by drought result in lower nodule biomass and N fixation rates (McCulloch et al., 2021). However, high temperature can inhibit the function of legume root nodules (Wang & Houlton, 2009), thus decreasing the N fixation capabilities of legumes and the effects on soil N cycling. Therefore, the positive effect of high MAP on legume effects offsets the negative influence of high MAT, leading to the result that legume effects on soil N cycling were not affected by climatic regions.

4.3 | Variations in the effects of legumes with experimental factors

We demonstrated that the increase in R_{min} caused by legumes was significantly greater in short-term experiments than in long-term experiments (Figure 2a), indicating that the effects of legumes on soil N cycling may decline over time. Such a variation between the duration of experiments was probably due to the effects of increased P limitation on legume growth during the later stage of the experiments. Legumes require large amounts of P to supply energy for N fixation (Mitran et al., 2018), and with increasing legume growth duration, soil P becomes depleted. For example, Zhang et al. (2021) found that soil P linearly decreased with increasing plantation age on the Loess Plateau. In our meta-analysis, legumes resulted in decreased available P in the short-term ($d_+ = -0.10$; $n = 15$) and long-term experiments ($d_+ = -0.60$; $n = 25$; Figure S5b), supporting this explanation. Some other N fixation-related nutrients (e.g., molybdenum, iron and manganese) might also decrease over the course of legume growth. Although this hypothesis was not confirmed herein because none of these elements was measured in any independent experiment collected in our global dataset, an early study in a woodland in central coastal Florida showed that a reduced availability of molybdenum explained the elevated CO_2-induced long-term decline in N fixation (Hungate et al., 2004), indirectly supporting this hypothesis. Therefore, the time dependence of legume effects on N cycling might be influenced by the progressive limitation of N fixation-related nutrients in soils. However, our dataset did not contain the information necessary to verify this mechanism, highlighting the necessity of exploring interactions among such factors in future research.

The significantly greater effects of legumes on R_{min} occurred during in situ incubation relative to laboratory incubation under standard temperature and moisture conditions (Figure 2). This might be because soil disturbance during soil transport to the laboratory (often with homogenization of the soil samples) and sample preparation methods (mixing, sieving, root removal) during laboratory incubation studies sufficiently change R_{min} (Risch et al., 2019, 2020), which decreases the relative importance of legume effects. In addition, the greater effects in in situ conditions might be ascribed to the diurnal variation in temperature and moisture under field conditions, which has been reported to accelerate soil N mineralization (Eviner et al., 2006; Wang et al., 2016). For example, Wang et al. (2016) showed that high temporal variations in temperature and moisture enhance soil N mineralization in montane grasslands of Central Europe.

4.4 | Legumes altered the dependence of soil net nitrogen mineralization on influencing factors

Our results demonstrated that legumes significantly altered the dependence of soil N cycling on N fertilization and environmental factors (Figure 5). N fertilization increased R_{min} in both legume and nonlegume soils, probably due to the increased soil N pools and reduced soil C/N ratios (Gruber & Galloway, 2008; Mueller et al., 2013). This result is consistent with previous results reported from global analyses (Hao et al., 2018; Risch et al., 2019, 2020) and experimental studies (Lu et al., 2011; Wei et al., 2019). However, in this study, we showed that the effect of N fertilization on R_{min} was lower in legume soils than in nonlegume soils (Figure 5), primarily because legumes can satisfy much of their own N needs by biological N fixation (Pirhofer-Walzl et al., 2012; Vitousek et al., 2013). Therefore, plants and microbes have a lower need for fertilizer N in legume treatments than in nonlegume treatments (Mueller et al., 2013; Wei et al., 2019), leading to the smaller effect of N fertilization on R_{min} in legume soils.

Our global analysis further showed that MAT was an important driver of R_{min} in treatments with and without legumes (Figure 5), mainly because higher temperatures may increase microbial metabolism and enzymatic activity, resulting in greater organic matter decomposition and N mineralization (Bai et al., 2013; Dai et al., 2020). For example, a previous global assessment showed that experimental warming resulted in a 52.2% increase in R_{min} (Bai et al., 2013). Increasing temperatures also indirectly affect N cycling processes by increasing net ecosystem production (Dai et al., 2020), which, in turn, increases inputs of root exudates and litter to soils (Dusenge et al., 2018). In our analysis, the effect of MAT on MBC was greater in nonlegume treatments than in legume treatments (Figure 5), mainly due to the higher C/N ratios of the litter in nonlegumes. Generally, high temperatures can promote plant growth and N cycling (Dai

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et al., 2020; Dusenge et al., 2018), but whether N is incorporated into microbial biomass or released as ammonium to the soil environment depends strongly on the C/N ratios of plant litter/exudate inputs (Mooshammer et al., 2014). The higher C/N ratios of the litter in nonlegumes would require microbes to acquire inorganic N from the soil (i.e., microbial immobilization) to meet their N assimilation needs when processing plant C inputs (Cleveland & Liptzin, 2007), thus resulting in a greater effect of MAT on MBC in nonlegume treatments than in legume treatments.

4.5 | Implications for nitrogen cycling and management

Our examination advances the current knowledge of the effects of legumes on terrestrial biogeochemical cycles by providing robust evidence that legumes have strong global impacts on soil N cycling. Across our dataset, soils with legumes had 67% higher R_{min} than those without legumes, and this value was significantly higher than the effect of N deposition. For instance, we observed 151% and 74% higher R_{min} in global grasslands and forests that contained legumes than in those without legumes, respectively, whereas N deposition ($10\,g\,N\,m^{-2}\,year^{-1}$) resulted in 34% (with grazers) and 66% (without grazers) increases in R_{min} in global grasslands (Risch et al., 2020) and had no impact on the mineral soils of northern temperate forests (Nave et al., 2009).

Since soil mineral N is the dominant form of N taken up by terrestrial plants and its concentration in soils is primarily regulated by N mineralization processes (Chen et al., 2021; Risch et al., 2020), the legume effect on R_{min} shown in this study, which varied with ecosystem types, could provide important implications for managed ecosystems (i.e., agricultural ecosystems) and for N limitation predictions in unmanaged ecosystems under the context of global change. For managed ecosystems with leguminous crops (i.e., solely leguminous crops, intercropped or rotated leguminous crops), the rate of chemical N fertilizers could be adequately reduced not only for upregulating the N fixation of legumes and satisfying the N need for plant growth (Liu et al., 2011; Menge et al., 2009), but also for preventing the loss of fertilizer N and related environmental problems (Drinkwater et al., 1998; Foyer et al., 2016), which is important because the global legume planting area has continually increased over the past half century (Figure S6). For unmanaged ecosystems, legumes are significantly affected by global change drivers, with increased abundance under warming (Cowles et al., 2016; Liao et al., 2017) and drought (Gei et al., 2018; Pellegrini et al., 2016) but decreased abundance under N enrichment conditions (Isbell et al., 2013; Tognetti et al., 2021). For this reason, legumes are increasingly and complexly intertwined with global change drivers in influencing N cycling (and N limitation) and even with the succession of unmanaged ecosystems, all of which call for an urgent understanding of such knowledge for better elucidation and prediction of ecosystem processes for a changing planet.

Natural processes (e.g., fire and grazing) impact N cycling in land ecosystems, and these processes are independent of legume effects but are dependent on ecosystem types and/or climatic regions. Frequent fire and disturbances (e.g., grazing) significantly change the cycling and availability of N (Dannenmann et al., 2018; Jiang et al., 2022) and can also remove large quantities of N from unmanaged ecosystems, which stimulates rapid regeneration of N-fixing species and individuals to replenish N deficits (Batterman et al., 2013; Vitousek et al., 2013). For example, Batterman et al. (2013) found that N-fixers dynamically act to replenish N deficits caused by disturbance events in tropical forests and soils. In addition, the initial stage of community succession (i.e., after fire and grazing) may not favor the growth of nonlegumes due to a limitation in N (Pellegrini et al., 2015), which may amplify the effects of legumes. Therefore, how these natural processes influence the effects of legumes should be further explicitly tested at the global scale.

AUTHOR CONTRIBUTIONS

Liping Qiu, Xiaorong Wei and Peter B. Reich designed the research; Xiaomei Gou collected the data; Xiaomei Gou and Xiaorong Wei analyzed the data. All authors contributed significantly to the writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Supporting Information and Figshare at https://doi.org/10.6084/m9.figshare.22655107

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