






PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Microbes drive global soil nitrogen mineralization and availability

Zhaolei Li¹ | Dashuan Tian¹  | Bingxue Wang¹ | Jinsong Wang¹  |
Song Wang^{1,2} | Han Y. H. Chen³  | Xiaofeng Xu⁴ | Changhui Wang⁵ |
Nianpeng He^{1,2}  | Shuli Niu^{1,2} 

¹Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

²College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China

³Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario, Canada

⁴Biology Department, San Diego State University, San Diego, California

⁵State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China

Correspondence

Shuli Niu, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China.
Email: sniu@igsrr.ac.cn

Funding information

Ministry of Science and Technology of China, Grant/Award Number: 2016YFC0501803; Postdoctoral Science Foundation of China, Grant/Award Number: 2018M641459; the CAS international collaboration program, Grant/Award Number: 131A11KYSB20180010; National Natural Science Foundation of China, Grant/Award Number: 31625006

Abstract

Soil net nitrogen mineralization rate (N_{\min}), which is critical for soil nitrogen availability and plant growth, is thought to be primarily controlled by climate and soil physical and/or chemical properties. However, the role of microbes on regulating soil N_{\min} has not been evaluated on the global scale. By compiling 1565 observational data points of potential net N_{\min} from 198 published studies across terrestrial ecosystems, we found that N_{\min} significantly increased with soil microbial biomass, total nitrogen, and mean annual precipitation, but decreased with soil pH. The variation of N_{\min} was ascribed predominantly to soil microbial biomass on global and biome scales. Mean annual precipitation, soil pH, and total soil nitrogen significantly influenced N_{\min} through soil microbes. The structural equation models (*SEM*) showed that soil substrates were the main factors controlling N_{\min} when microbial biomass was excluded. Microbe became the primary driver when it was included in *SEM* analysis. *SEM* with soil microbial biomass improved the N_{\min} prediction by 19% in comparison with that devoid of soil microbial biomass. The changes in N_{\min} contributed the most to global soil NH_4^+ -N variations in contrast to climate and soil properties. This study reveals the complex interactions of climate, soil properties, and microbes on N_{\min} and highlights the importance of soil microbial biomass in determining N_{\min} and nitrogen availability across the globe. The findings necessitate accurate representation of microbes in Earth system models to better predict nitrogen cycle under global change.

KEYWORDS

croplands, dominant factor, microbial biomass, natural ecosystems, nitrogen availability, nitrogen mineralization, soil properties

1 | INTRODUCTION

Nitrogen is a pivotal element for plant growth and the total amount of resident nitrogen is estimated at 133–140 Pg for the upper 100 cm soil (Batjes, 1996). The dominant component of soil nitrogen is in organic form (Schulten & Schnitzer, 1997), but plants primarily take up inorganic nitrogen and can only absorb a small portion of low-molecular-weight

organic nitrogen (e.g., glycine) under extreme conditions (Nasholm et al., 1998). Only when organic nitrogen is mineralized to inorganic nitrogen may it be easily taken up by plants (Ashton, Miller, Bowman, & Suding, 2010). Thus, the rate of organic nitrogen mineralization (N_{\min}) is a critical parameter controlling ecosystem productivity (Keuper et al., 2017). It is imperative to unravel the controlling factors and mechanisms that underlie changes in soil N_{\min} on a global scale.

Soil N_{min} rates are believed to be primarily controlled by climate and soil properties on a global scale (Liu et al., 2017). The rate of N_{min} increases with mean annual temperature (Dawes, Schlegel, Hattenschwiler, Rixen, & Hagedorn, 2017; Rustad, Campbell, & Marion, 2001; but Auyeung, Suseela, & Dukes, 2013) and precipitation (Burke, Lauenroth, & Parton, 1997). Soil physical and/or chemical properties have been reported to have inconsistent effects on N_{min} . For example, Hassink (1994) found that soil N_{min} was negatively correlated to clay and silt content. However, Franzluebbers (1999) reported that the soil clay content had positive or neutral effect on N_{min} . The N_{min} is generally suppressed by soil acidification (Liu et al., 2016) but increases with addition of organic matter and soil substrate (Ameloot, Sleutel, Das, Kanagaratnam, & Neve, 2015; Rousk, Michelsen, & Rousk, 2016). Besides climatic and soil properties, soil resident biotic factors should directly affect soil N_{min} (Verhoef & Brussaard, 1990). Changes in soil microbial biomass have been reported to have a profound impact on N_{min} (Hassink, 1995), and variations in N_{min} are primarily attributable to changes in soil microbial biomass following land use change (McMillan, Quideau, Mackenzie, & Biryukova, 2007). Nevertheless, previous experimental studies usually focused on the individual effect of these abiotic and biotic factors, although they are eventually interacting with each other. A comprehensive understanding of the relative importance of various factors and their impacting pathways on N_{min} is lacking. Furthermore, terrestrial ecosystems differ in terms of climate, soil physical properties, soil organic matters, and soil microbial biomass (Xu, Thornton, & Post, 2013), the impacts of these factors on N_{min} might vary among ecosystems. However, it remains unclear about the different roles of these factors in different ecosystems.

Recent studies have attempted to develop empirical models to predict changes in soil N_{min} . Liu et al. (2017) proposed N_{min} as a function of soil properties (*i.e.*, clay and pH) and substrate (*i.e.*, soil organic matter) on a global scale in the structural equation model (SEM), and the climatic variables influenced N_{min} through changing substrates and/or soil properties. An experimental study that sampled 84 soils across North America demonstrated that soil total nitrogen and clay content directly influenced N_{min} , whereas the mean annual precipitation affected N_{min} *via* altering soil substrates (Colman & Schimel, 2013). Although soil N_{min} is conceptually linked to soil microbes (Schimel & Bennett, 2004), the role of soil microbes has not been well presented in predicting soil N_{min} over large spatial scales (Colman & Schimel, 2013; Liu et al., 2017). A previous study on carbon cycling revealed that when soil microbial biomass carbon was incorporated into a model, the accuracy of carbon prediction could be significantly improved (Wieder, Bonan, & Allison, 2013). Therefore, we proposed a new hypothetical framework that incorporates the role of microbial biomass and its interactions with climatic and soil properties to improve the N_{min} prediction across large spatial scales (Figure 1). In this framework, climatic variables, soil properties, and substrates might directly influence N_{min} ; however, more importantly, these factors will indirectly affect N_{min} *via* changes in soil microbial biomass.

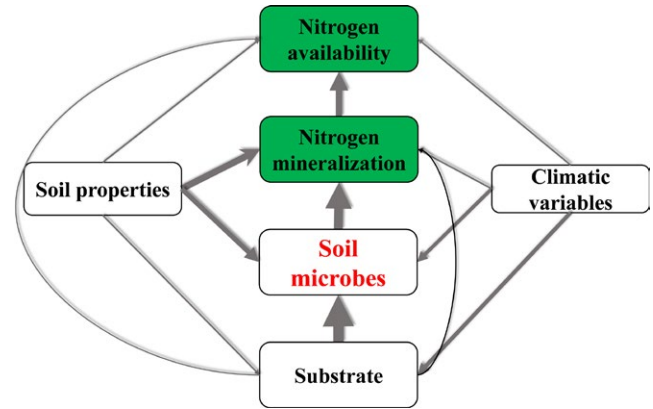


FIGURE 1 A proposed conceptual framework for net nitrogen mineralization (N_{min}) changes on a global scale. Gray arrows refer to the assumed relationships between two variables. The width of the gray line refers to the degree of the relationship between the two. The global variations of nitrogen mineralization rate were influenced by climatic variables, soil properties, substrates, and soil microbes, where soil microbes played a dominant role in N_{min} among these factors. Subsequently, the N_{min} affected the global soil nitrogen availability [Colour figure can be viewed at wileyonlinelibrary.com]

To test the above hypothesis, we compiled 1565 observational data points from 198 published articles and addressed three specific questions: 1. What is the role of soil microbial biomass in determining global N_{min} when compared with climate, soil properties, and substrates on a global scale? 2. Will the model with microbial biomass strikingly improve the capacity to predict soil N_{min} and its availability on a global scale? 3. Do the microbial roles differ among ecosystem types in regulating N_{min} ?

2 | MATERIALS AND METHODS

2.1 | Data collection, operation, and overview

Data were collected by searching all published peer-reviewed articles that investigated soil net N_{min} using the Web of Science (<http://apps.webofknowledge.com>) and the China National Knowledge Infrastructure Database (<http://www.cnki.net/>), up to April 1, 2018. Three criteria were used to screen literatures: (a) Potential net N_{min} rates were reported; (b) N_{min} was measured in laboratory with top 0–10 cm soil (mostly in grassland and cropland) or top 0–15 cm soil (mostly in forests); (c) There was an explicit description of the incubation temperature for N_{min} . Site-specific data such as latitude, longitude, mean annual temperature, mean annual precipitation, soil texture, pH, total soil nitrogen, inorganic nitrogen, soil microbial biomass, ecosystem type, and replicates were also obtained from the original study, and all original data were extracted from the text, tables, and figures. While the data were presented by figures in the papers, the software program, GetData (version 2.22), was employed for data extraction.

Our selection process yielded 198 papers, from which we compiled a dataset with 1565 observations. When the mean annual

temperature and precipitation were not reported in these papers, we obtained and integrated these data from the climatic database at <http://www.worldclim.org/using-geographic-information> (i.e. latitude and longitude). The incubation temperature for N_{\min} measurement was mostly at 25°C (534 observations out of 1565). Therefore, all N_{\min} s were adjusted to 25°C using the temperature sensitivity (Q_{10}) of N_{\min} published by Liu et al. (2017). The adjustment formula was:

$$N_{\min 2}/N_{\min 1} = Q_{10}^{(25-T_1)/10} \quad (1)$$

where $N_{\min 1}$ and $N_{\min 2}$ are the reported N_{\min} and recalculated N_{\min} at 25°C, respectively. T_1 is the incubation temperature for $N_{\min 1}$.

The dataset encompassed four terrestrial ecosystem types, namely, croplands, forests, grasslands, and wetlands. The number of observations for the croplands, forests, grasslands, and wetlands was 736, 269, 317, and 84, respectively. The sites in this dataset were geographically distributed from 46.32°S to 78.17°N latitude, and from 159.5°W to 176°E longitude. The climatic conditions ranged from -9.8 to 30.1°C for the mean annual temperature, and from 51 to 4,000 mm for the mean annual precipitation. Soil clay content ranged from 1% to 81%.

2.2 | Statistical analyses

A linear mixed-effect model was employed to examine the relationships between N_{\min} and climatic variables (mean annual temperature and precipitation), soil properties (pH, clay content), substrate (total soil nitrogen), and soil microbial biomass (microbial biomass carbon and nitrogen). For each variable (X) except for pH, we tested the relationship between $\ln(N_{\min})$ and $\ln X$ using the model:

$$\ln(N_{\min}) = \beta_0 + \beta_1 \times \ln X + \pi_{\text{study}} + \varepsilon \quad (2)$$

where β_0 , β_1 , π_{study} , and ε are the intercept, coefficient, the random effect, and sampling error, respectively. The random effect accounts for the effects among observations within each "study." To compare the responses of N_{\min} to variables across ecosystems, the data were standardized (z-score normalization), after which formula 2 was used. Similarly, the regression between the ammonium content ($\text{NH}_4^+\text{-N}$) and N_{\min} on a global scale was examined using the model 3:

$$\ln(\text{NH}_4^+ - \text{N}) = \beta_0 + \beta_1 \times \ln N_{\min} + \pi_{\text{study}} + \varepsilon \quad (3)$$

The data were standardized and the responses of $\text{NH}_4^+\text{-N}$ to N_{\min} were subsequently examined in each ecosystem type. We conducted the analyses using the maximum likelihood estimation with the *lme4* package (Bates, Machler, Bolker, & Walker, 2018). The *emmeans* package was used to compare the responses of $\text{NH}_4^+\text{-N}$ to N_{\min} among ecosystem types (Lenth, 2018). For each ecosystem type, the slopes between N_{\min} and variables (climate, soil properties, substrate, and microbial biomass) were extracted

and plotted into a scatter figure with 95% confidence intervals. Likewise, the scatter figure showing the relationship between $\text{NH}_4^+\text{-N}$ and N_{\min} in different ecosystems was charted by the same approach.

2.3 | Structural equation modeling

We used SEM approach to evaluate how N_{\min} and soil nitrogen availability were influenced by environmental factors and their interactions. Specifically, to evaluate the influence of soil microbes on N_{\min} and soil nitrogen availability, we independently ran two SEM models without or with microbial biomass. In the first model (without soil microbial biomass), we tested the relative influences of climatic variables, soil properties, and substrates on N_{\min} and soil nitrogen availability. In the second model we examined to what extent the role of microbial biomass played on N_{\min} . Because there were no significant relationships of soil N_{\min} with mean annual temperature or soil clay in bivariate regressions, mean annual temperature and soil clay were not included in SEMs. We assessed the conceptual model by the goodness-of-fit statistics and used the lowest AIC value to select the optimal model. The SEM analyses were performed with *piecewiseSEM* package using the maximum likelihood estimation method (Lefcheck, 2015). All statistical analyses in this study were performed on the R platform (version 3.5.0).

3 | RESULTS

3.1 | Bivariate relationships of N_{\min} with climatic variables, soil properties, substrate, and microbial biomass on a global scale

Soil N_{\min} increased significantly with the mean annual precipitation on a global scale ($R^2 = 0.272$, $p < 0.001$; Figure 2a). There was no significant relationship between N_{\min} and the mean annual temperature ($R^2 = 0.271$, $p = 0.687$; Supporting information Figure S1). Soil N_{\min} was negatively correlated with soil pH ($R^2 = 0.269$, $p = 0.012$; Figure 2b) and positively correlated with total soil nitrogen ($R^2 = 0.299$, $p < 0.001$; Figure 2c), but had no significant correlation with soil clay content ($R^2 = 0.302$, $p = 0.323$; Supporting information Figure S2).

Soil N_{\min} significantly increased with microbial biomass on a global scale (Figure 3). Specifically, N_{\min} increased with soil microbial biomass carbon with a slope of 0.601 ($R^2 = 0.407$, $p < 0.001$), and increased with soil microbial biomass nitrogen with a slope of 0.335 ($R^2 = 0.265$, $p < 0.001$). The variation of N_{\min} was ascribed more to microbial biomass carbon (Figures 2 and 3).

3.2 | The relative contribution of climatic variables, soil properties, substrate, and microbial biomass to N_{\min} variation

The SEM without soil microbial biomass showed that N_{\min} did not have significant relationships with mean annual precipitation or soil pH, with the standardized coefficients being -0.04 ($p = 0.665$) and

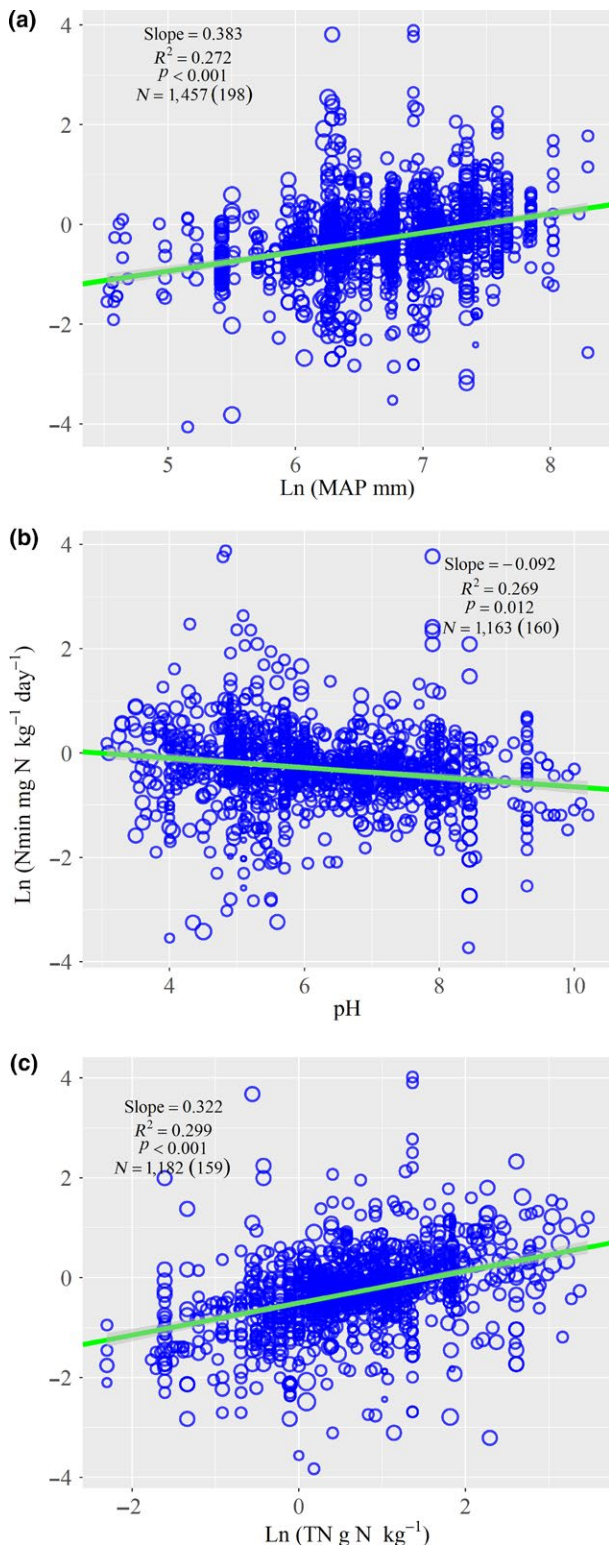


FIGURE 2 Bivariate relationships of soil net nitrogen mineralization rate (N_{\min}) with mean annual precipitation (MAP), soil pH, and total soil nitrogen content (TN) on a global scale. The green lines and thicker gray shaded lines represent the mean and 95% confidence intervals of the slope regressed by the linear mixed-effect model. The larger blue circles refer to the larger number of replicates, ranging from 1 to 15. The number of observations is after N without parentheses, and the number of studies is in parentheses [Colour figure can be viewed at wileyonlinelibrary.com]

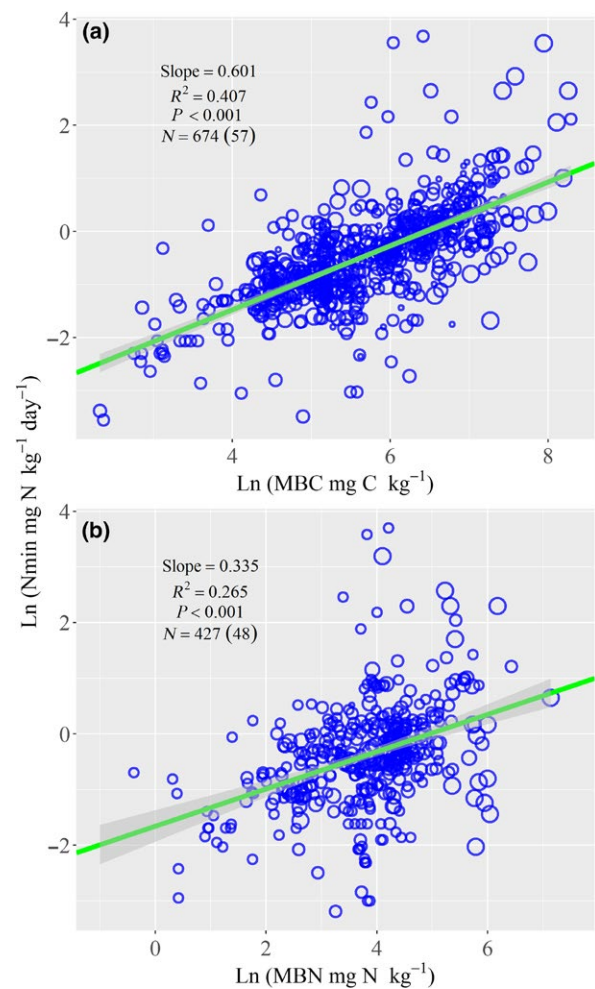


FIGURE 3 Bivariate relationships of soil nitrogen mineralization (N_{\min}) and soil microbial biomass carbon (MBC) and nitrogen (MBN) on a global scale. The green lines and thicker gray shaded lines are the mean and 95% confidence intervals of the slope regressed by the linear mixed-effect model. The larger blue circles refer to the larger number of replicates, ranging from 1 to 15. The number of observations is after N without parentheses, and the number of studies is in parentheses [Colour figure can be viewed at wileyonlinelibrary.com]

-0.23 ($p = 0.111$), respectively (Figure 4a). Conversely, there were significant relationships between N_{\min} and total soil nitrogen (the standardized coefficient = 0.45 , $p < 0.001$), which suggested that N_{\min} was more tightly correlated to the substrate, relative to climatic variables and soil properties. In addition, the total soil nitrogen content was significantly related to mean annual precipitation ($p < 0.001$), but not to pH ($p = 0.346$).

When soil microbial biomass was incorporated into the SEM, N_{\min} decreased with soil pH at a standardized coefficient of -0.42 ($p = 0.004$). The relationship between N_{\min} and the total soil nitrogen became insignificant ($p = 0.532$) and the standardized coefficient decreased from 0.45 (Figure 4a) to 0.08 (Figure 4b). Noticeably, the soil microbial biomass was significantly affected by the mean annual precipitation, soil pH, and total soil nitrogen on a global scale, with the coefficients being -0.24 ($p < 0.001$), 0.30 ($p = 0.007$), and 0.68 ($p < 0.001$), respectively. In turn, greater soil

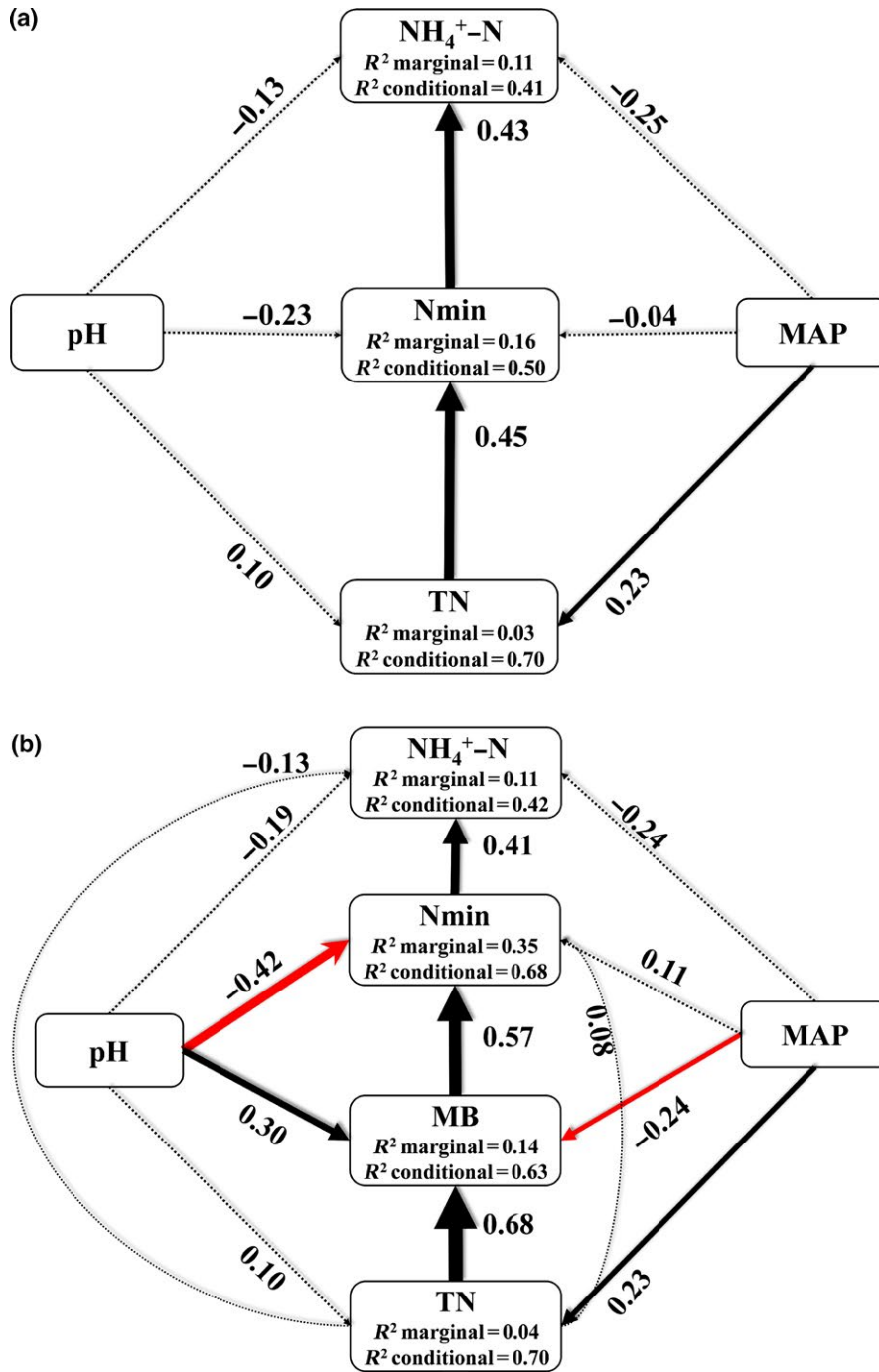


FIGURE 4 Structural equation models (SEM) without (a) or with soil microbial biomass (MB) (b) revealing the influences of mean annual precipitation (MAP), soil pH, total soil nitrogen (TN), MB on soil nitrogen mineralization (N_{min}), and nitrogen availability (NH₄⁺-N). The solid lines refer to significant relationships, whereas the dashed lines refer to nonsignificant relationships, where the significance level was set at $\alpha = 0.05$. Arrows represent the directional influence of one variable upon another. Black arrows represent positive relationships and red arrows represent negative relationships. Numbers beside the arrows are standardized coefficients. *R*² marginal and *R*² conditional refer to the degree of variation of the variable interpreted by all paths from the single fixed effects, and combination from the fixed and random effects, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

microbial biomass significantly stimulated N_{min} (standardized coefficient = 0.57, $p < 0.001$). The SEM model including soil microbial biomass significantly enhanced the N_{min} predictability on a global scale, as the total variances for N_{min} that explained by the fixed factors, improved from 16% (Figure 4a) to 35% (Figure 4b).

3.3 | Attributes of N_{min} variations in different ecosystems

Soil N_{min} significantly increased with microbial biomass carbon in all ecosystem types (all $p < 0.05$; Figure 5). Specifically, in

croplands, N_{min} increased with mean annual precipitation, total soil nitrogen, microbial biomass carbon, and microbial biomass nitrogen (all $p < 0.05$), but decreased with soil pH ($p < 0.001$). Furthermore, the response of N_{min} was more sensitive to microbial biomass carbon than to total soil nitrogen ($p = 0.002$), which suggested that soil microbial biomass played a more important role in determining N_{min} than substrate in croplands. The response of N_{min} to microbial biomass carbon was similar with that to microbial biomass nitrogen ($p = 0.66$) in croplands.

In forests and grasslands, N_{min} also significantly increased with the mean annual precipitation, total soil nitrogen, microbial biomass

carbon, and microbial biomass nitrogen, but decreased with pH (all $p < 0.05$). The responses of N_{\min} to soil microbial biomass appeared to be more sensitive than to other variables, which was reflected by the greater slopes of N_{\min} against soil microbial biomass than those of N_{\min} against other variables (all $p < 0.05$). In wetlands, N_{\min} significantly increased with microbial biomass carbon but decreased with soil pH (both $p < 0.05$). There were no significant relationships between N_{\min} and mean annual precipitation, total soil nitrogen and microbial biomass nitrogen ($p = 0.58, 0.06$, and 0.13 , respectively).

3.4 | The relationships between soil nitrogen availability and N_{\min}

Soil ammonium content increased significantly with N_{\min} on a global scale with the slope being 0.21 ($R^2 = 0.476$, $p < 0.001$; Figure 6a). This relationship was consistent across all ecosystem types (all $p < 0.05$; Figure 6b). The slopes were 0.11 for croplands, 0.44 for forests, 0.59 for grasslands, and 0.34 for wetlands, respectively. The SEM results revealed that soil NH_4^+ -N content was not significantly correlated with the mean annual precipitation ($p = 0.058$), soil pH ($p = 0.291$), or total soil nitrogen ($p = 0.407$) (Figure 4). However, the relationships between soil NH_4^+ -N content and N_{\min} were significant in both

models (the standardized coefficient was 0.43 and 0.41 , respectively; $p < 0.001$ for both models). Higher total nitrogen levels in the soil significantly increased the soil microbial biomass and subsequently the N_{\min} , which resulted in higher soil nitrogen availability (Figure 4b). Furthermore, the fixed factors in model could explain 11% of the

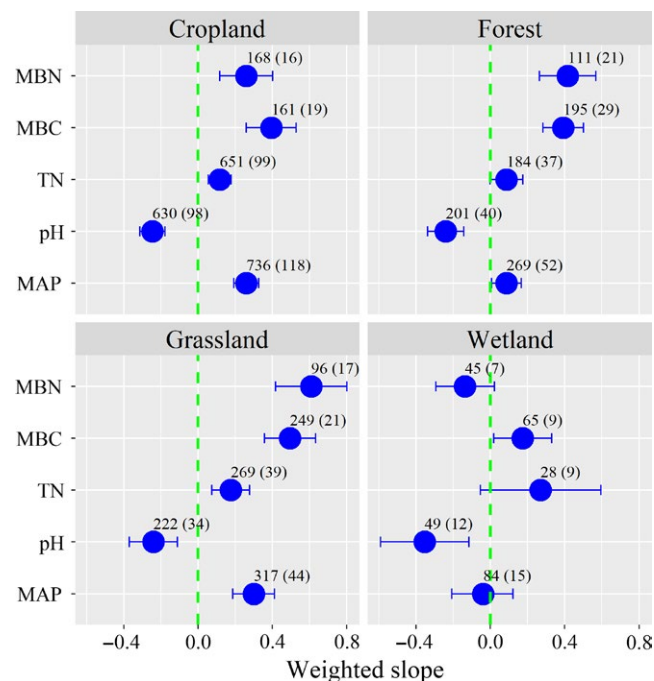


FIGURE 5 Weighted slopes of the relationship from the linear mixed-effect model between soil nitrogen mineralization (N_{\min}) and MAP, pH, TN, MBC, MBN following the data normalization across ecosystems. The blue dots with bars are mean \pm 95% confidence intervals of the weighted slope between N_{\min} and MAP, pH, TN, MBC, and MBN. The number of observations is beside each attribute without parentheses, and the number of studies is in parentheses. MAP, TN, MBC, and MBN represent mean annual precipitation, total soil nitrogen, soil microbial biomass carbon, and soil microbial biomass nitrogen, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

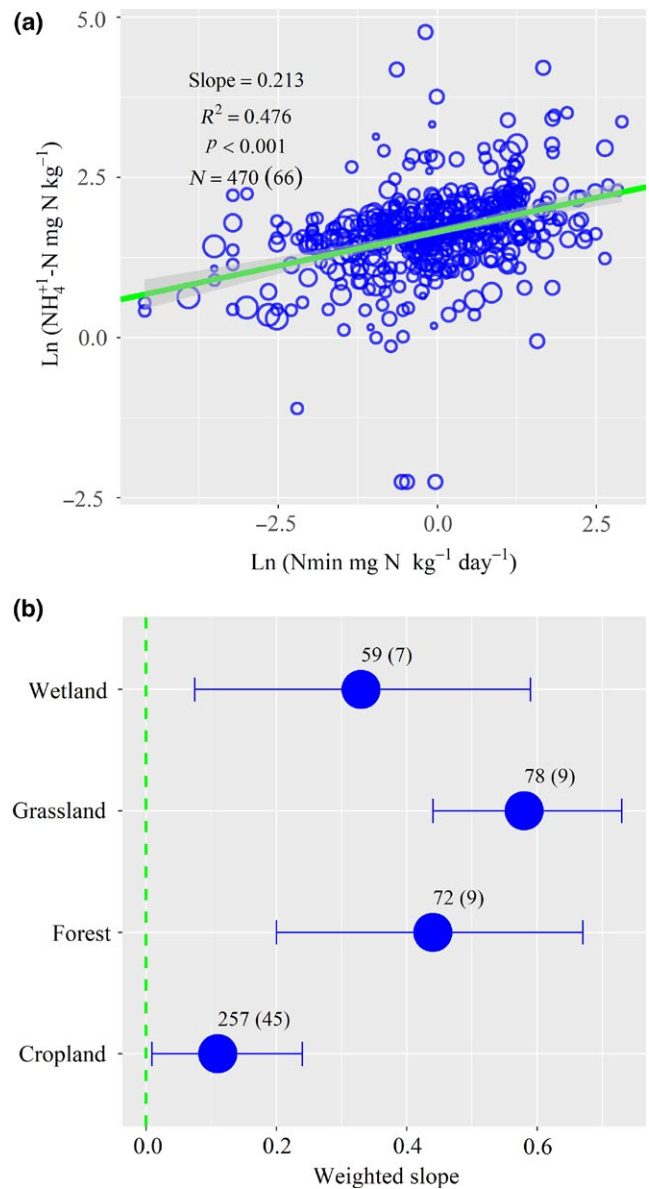


FIGURE 6 Bivariate relationship between soil ammonium content (NH_4^+ -N) and soil nitrogen mineralization (N_{\min}) on a global scale (a) and the weighted slopes distilled from the regression using normalizing data between NH_4^+ -N and N_{\min} across ecosystems (b). The green lines and thicker gray shaded lines are the mean and 95% confidence intervals of the slope regressed by the linear mixed-effect model. The larger blue circles refer to the larger number of replicates, ranging from 1 to 15. The number of observations is in parentheses (a). The blue dots with bars are mean \pm 95% confidence intervals of the weighted slopes. The values beside each dot without parentheses are the number of observations, and those in parentheses are the number of studies (b) [Colour figure can be viewed at wileyonlinelibrary.com]

total variances for $\text{NH}_4^+\text{-N}$, and N_{\min} contributed the most to the soil $\text{NH}_4^+\text{-N}$ content in contrast to the other variables on a global scale.

The responses of soil $\text{NH}_4^+\text{-N}$ content were more sensitive to N_{\min} in natural ecosystems (*i.e.* forests, grasslands) relative to that in croplands. The slope of soil $\text{NH}_4^+\text{-N}$ against N_{\min} in croplands was significantly less than that in grasslands ($p < 0.001$) and marginally significantly less than that in forests ($p = 0.08$). There was no significant difference in magnitudes between croplands and wetlands ($p = 0.46$). The slopes did not significantly differ from one another among natural ecosystems (forests vs. grassland, $p = 0.72$; forests vs. wetlands, $p = 0.93$; grasslands vs. wetlands, $p = 0.35$).

4 | DISCUSSION

This study provides a comprehensive evaluation of the determinants of global N_{\min} with a focus on soil microbial biomass. Consistent with our proposed conceptual framework (Figure 1), the results demonstrated that soil microbial biomass predominantly controlled the variability of N_{\min} and subsequently soil nitrogen availability at a global scale. Climate, soil properties and substrates influenced N_{\min} via their impacts on soil microbial biomass. The study highlights the importance of microbial biomass in determining soil nitrogen cycling, which challenges the conventional view that climate and soil properties are the dominant drivers of soil N_{\min} (Liu et al., 2017) and advances our current understanding on the global patterns of nitrogen cycle (Canfield, Glazer, & Falkowski, 2010; Niu et al., 2016). The findings suggest that changes in soil microbial biomass under global change would result in profound consequences on ecosystem processes by changes in soil N_{\min} .

4.1 | The dominant role of soil microbe biomass in determining N_{\min} on a global scale

Soil microbial biomass played a more important role in determining changes in N_{\min} than climate and soil physical and/or chemical properties on a global scale. The dominant role of microbes can be explained in the following three ways. First, a large portion of the mineralizable nitrogen (55%–89%) was derived from the microbial biomass nitrogen (Bonde, Schnurer, & Rosswall, 1988). The microbial biomass usually has a high turnover rate, ranging from 0.81–0.87 per year (Goyal, Mishra, Dhankar, Kapoor, & Batra, 1993), which provides large amount of substrate for nitrogen mineralization. This is supported by some experiments, which showed that the stimulation of N_{\min} was likely due to the necromass of microbial biomass (Mikha, Rice, & Milliken, 2005). Second, soil N_{\min} was catalyzed by a series of enzymes, including protease, urease, and transaminase, *etc.*, which are directly correlated with the size of microbial biomass (Ajwa, Dell, & Rice, 1999). For example, the activities of urease and amidase were more closely associated with the soil microbial biomass than the soil organic matters (Nayak, Babu, & Adhya, 2007), and the accumulated mineralized nitrogen was significantly related to the activity of β -glucosaminidase

(Ekenler & Tabatabai, 2002). Third, higher microbial biomass might benefit the reactivation or the reproduction of microbes, which would stimulate soil N_{\min} .

Soil pH was the second most important factor that affected N_{\min} on a global scale, including the indirect effects through changing soil microbial biomass and the direct effects through changing soil metabolic and enzymatic activities. Soil pH determined the geographical patterns of soil bacteria (Fierer & Jackson, 2006), fungi (Tedersoo et al., 2014) and microbial metabolic quotient (Xu, Schimel, & Janssens, 2017). For example, at two agricultural sites, soil microbial biomass increased with pH ranging from 3 to 7 ($R^2 = 0.32\text{--}0.62$) (Kemmitt, Wright, Goulding, & Jones, 2006). In soil pH manipulation experiments, the artificial promotion of pH (soil liming) led to the increments of microbial biomass carbon ($R^2 = 0.80$) (Pietri & Brookes, 2008), and the augmentation of soil acidification frequently reduced soil microbial biomass (Pennanen et al., 1998). Soil microbial nitrogen was also positively related to pH in a long-term experiment (Pietri & Brookes, 2008). However, the microbial metabolic activity might decrease with pH. For example, the fungal growth decreased by 5-fold as pH increased from 4.5 to 8.3 (Rousk, Brookes, & Baath, 2009), and the hydrolyzed nitrogen extracted by a phosphate-borate buffer decreased under higher pH (Curtin, Campbell, & Jalil, 1998). Ammonification was significantly suppressed and the total mineralized arginine-nitrogen was slightly lessened with increasing pH (Kemmitt et al., 2006). Another potential reason was that higher pH decreased the activities of the enzymes that directly regulated N_{\min} . For instance, the activity of urease decreased when soil pH increased from 4.5 to 8.5 (Singh & Nye, 1984). The activities of some protease were optimal under acidic conditions (Kamimura & Hayano, 2000). Consistently, soil $\text{NH}_4^+\text{-N}$ content decreased from 68.6 to 0 mg/kg under pH ranging from 6.8 to 8.1 (Pathak & Rao, 1998). The response of N_{\min} to pH was somewhat different from that of carbon mineralization (Pietri & Brookes, 2008). This might have been caused by the different responses of enzymes that catalyze the mineralization of organic matter to soil pH. For example, phenol oxidase and peroxidase increased (slope = 0.91, 0.63), whereas β -N-acetylglucosaminidase decreased (slope = -0.54) with pH from 4 to 9 on a global scale (Sinsabaugh et al., 2008).

The mean annual precipitation and total soil nitrogen initially influenced soil microbial biomass and subsequently N_{\min} . The mean annual precipitation might significantly affect microbial abundance on a global scale (Serna-Chavez, Fierer, & Vanbodegom, 2013). It was reported that soil microbial biomass tended to decrease with mean annual precipitation, which was 35.7 mmol C/kg in tropical forests and 44.7 mmol C/kg in the temperate forests (Xu et al., 2013). Although the overall effect of mean annual precipitation on soil N_{\min} was minor (-0.03) at the global scale, it significantly influenced soil N_{\min} through changing microbial biomass (-0.14). It was very clear that soils with additional substrates enhanced soil microbial biomass on a global scale (Kallenbach & Grandy, 2011), which could expedite N_{\min} .

Global soil N_{\min} explained most of variation in soil nitrogen availability. Soil $\text{NH}_4^+\text{-N}$, which is the product of N_{\min} , was subsequently

transformed to nitrate (Butler et al., 2012). Therefore, N_{\min} might well predict in situ nitrogen availability (Osterholz et al., 2017). Other variables, such as mean annual precipitation, soil pH, and total soil nitrogen explained little of the changes in soil nitrogen availability, however, they had considerable impacts on soil microbial biomass and thus N_{\min} (Figure 4), which could in turn influence the availability of soil nitrogen.

4.2 | Differences among ecosystem types

Although soil microbial biomass was the most important factor in determining soil N_{\min} for all the ecosystem types, the control of soil microbial biomass on N_{\min} was greater in forests and grasslands than that in croplands. Croplands were under severe anthropogenic perturbation such as tillage and fertilization, where these practices thereby generally impacted soil microbial biomass. For instance, soil microbial biomass decreased by 37%–50% under tillage (Balota, Colozzi, Andrade, & Dick, 2004); the microbial biomass significantly declined with the rate of nitrogen addition ($R^2 = 0.93$ – 0.98) (Lee & Jose, 2003) and a meta-analysis found that nitrogen fertilization reduced microbial biomass by 6.4%–15% on average on a global scale (Treseder, 2008). It suggests that human management lessened the relationship between N_{\min} and soil microbial biomass in croplands.

A distinct pattern of N_{\min} emerged in wetlands compared with other ecosystems. Except for soil microbial biomass carbon and pH, other factors did not exhibit any significant relationship with N_{\min} . This may be due to water saturation in wetlands, which could significantly impede soil ventilation. Although N_{\min} might occur under waterlogging (Lober & Reeder, 1993), anaerobic environment generally depressed N_{\min} (Wang, Chalk, Chen, & Smith, 2001). The specific conditions of wetlands distorted the correlations between N_{\min} and the variables in comparison with other ecosystems.

Soil nitrogen availability appeared to be more sensitive to N_{\min} in natural ecosystems in contrast to croplands that are often anthropogenically fertilized, with an ammonium usage of ~100 Tg per year (Erisman, Sutton, Galloway, Klimont, & Winiwarter, 2008). This might impact the soil nitrogen availability to a significant degree. In contrast, the accessibility of soil nitrogen relied primarily on N_{\min} in natural ecosystems.

4.3 | Implications

Understanding the pattern of soil N_{\min} under global change is important for modeling biogeochemical cycle and its feedback to climate (Thornton, Lamarque, Rosenbloom, & Mahowald, 2007). Our work highlights the important role of soil microbial biomass for controlling global soil N_{\min} . This perspective provides the basis for model parameterization of nitrogen cycling. Models with soil microbial biomass can substantially improve the prediction in soil N_{\min} and nitrogen availability by incorporating relationships between microbial biomass and climate and soil properties (Figure 4). The models of soil nitrogen cycle are moving from those mostly on

the basis of the interactions between different soil nitrogen pools (e.g., total soil nitrogen, ammonium, and nitrate; Chambers, Lord, Nicholson, & Smith, 1999) toward microbes-driven nitrogen cycling (Brovelli, Batlle-Aguilar, & Barry, 2012). Thus, the biogeochemical models incorporating soil microbial biomass and its interactions with climate and soil properties will largely improve the predictability of soil nitrogen dynamics. Furthermore, the incorporation of soil nitrogen mineralization or availability into Earth system models is urgently needed to more accurately predict carbon dynamics and its feedback to climate change (Thornton et al., 2009). The models of carbon cycle are improving toward incorporating soil nitrogen cycling (von Bloh et al., 2018; Zaehle et al., 2010). We expected that the findings in this study would provide empirical evidence and basis for parameterizing and improving the carbon models in Earth system models.

Our study also suggests that changes in microbial biomass in the context of global change will ultimately affect soil nitrogen availability through altering N_{\min} . Nitrogen deposition decreased soil microbial biomass carbon by 15% (Treseder, 2008) and might in turn suppress N_{\min} . The residue amendments in croplands increased the microbial biomass carbon by 36% (Kallenbach & Grandy, 2011), which could also have a cascading effect on N_{\min} and nitrogen availability. The alterations in soil nitrogen availability would result in profound effects on ecosystem processes. The potential stimulation of N_{\min} upon increases in microbial biomass carbon under climate warming might contribute to augments in gross ecosystem photosynthesis (Lu et al., 2013). The stimulation of soil microbial biomass (c. 20%) under increased precipitation in grassland may elicit greater available soil nitrogen to drive increments of net primary production (Liu, Zhang, & Wan, 2009).

About 30% of the variations in N_{\min} remain unexplained in our model, which may be attributable to the shifts in microbial community structures. Some studies pointed out that N_{\min} was negatively correlated with fungal and gram-negative bacteria (Fraterrigo, Balser, & Turner, 2006), and even fungi-to-bacteria ratio (Hogberg, Chen, & Hogberg, 2007). Unfortunately, microbial community was not included in this study because of data paucity. In the context of global change, soil microbial community compositions have been altered by climate change (Castro, Classen, Austin, Norby, & Schadt, 2010) and/or anthropogenic disturbances (Jangid, Williams, & Franzluebbers, 2008), which might ultimately lead to changes in N_{\min} and the availability of soil nitrogen. Thus, future studies that account for microbial community structures hold promise for enhancing confidence in the prediction of available soil nitrogen in response to future global changes.

This study highlights the importance of soil microbes in controlling the global net mineralization rate and soil nitrogen availability. The SEM model incorporating soil microbial biomass improved prediction of mineralization rate by 19% on a global scale. Moreover, climatic and soil factors, such as mean annual precipitation and total soil nitrogen, influenced mineralization rate through changing soil microbial biomass, but did not directly determine it. The availability of soil nitrogen for plant uptake can be largely predicted by

mineralization rate on a global scale, particularly in natural ecosystems. In the future, we need data on soil microbial community structures to further enrich our understanding of microbial influences on mineralization rate. The importance of microbes in controlling mineralization rate revealed in this study is crucial for our understanding of nitrogen cycling and its underlying mechanisms. It also highlights the need to explicitly incorporate microbes into biogeochemical models to improve prediction of global nitrogen cycle.

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (31625006), the Ministry of Science and Technology of China (2016YFC0501803), the CAS international collaboration program (131A11KYSB20180010), and the Postdoctoral Science Foundation of China (2018M641459).

CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

S.N. designed the research; Z.L. performed the analysis; and Z.L., S.N. wrote the first draft. All the authors contributed to the writing of this paper.

ORCID

Dashuan Tian  <https://orcid.org/0000-0001-8023-1180>

Jinsong Wang  <https://orcid.org/0000-0002-3425-7387>

Han Y. H. Chen  <https://orcid.org/0000-0001-9477-5541>

Nianpeng He  <https://orcid.org/0000-0002-0458-5953>

Shuli Niu  <https://orcid.org/0000-0002-2394-2864>

REFERENCES

- Ajwa, H. A., Dell, C. J., & Rice, C. W. (1999). Changes in enzyme activities and microbial biomass of tallgrass prairie soil as related to burning and nitrogen fertilization. *Soil Biology & Biochemistry*, 31, 769–777. [https://doi.org/10.1016/S0038-0717\(98\)00177-1](https://doi.org/10.1016/S0038-0717(98)00177-1)
- Ameloot, N., Sleutel, S., Das, K. C., Kanagaratnam, J., & De Neve, S. (2015). Biochar amendment to soils with contrasting organic matter level: Effects on N mineralization and biological soil properties. *Global Change Biology Bioenergy*, 7, 135–144. <https://doi.org/10.1111/gcbb.12119>
- Ashton, I. W., Miller, A. E., Bowman, W. D., & Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: Plant partitioning of chemical N forms. *Ecology*, 91, 3252–3260. <https://doi.org/10.1890/09-1849.1>
- Auyeung, D. S. N., Suseela, V., & Dukes, J. S. (2013). Warming and drought reduce temperature sensitivity of nitrogen transformations. *Global Change Biology*, 19, 662–676. <https://doi.org/10.1111/gcb.12063>
- Balota, E. L., Colozzi, A., Andrade, D. S., & Dick, R. P. (2004). Long-term tillage and crop rotation effects on microbial biomass and C and N mineralization in a Brazilian Oxisol. *Soil & Tillage Research*, 77, 137–145. <https://doi.org/10.1016/j.still.2003.12.003>
- Bates, D., Machler, M., Bolker, B., & Walker, S. (2018). *Fitting linear mixed-effects models using lme4*. arXiv:1406.5823.
- Batjes, N. H. (1996). Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science*, 47, 151–163. <https://doi.org/10.1111/j.1365-2389.1996.tb01386.x>
- Bonde, T. A., Schnurer, J., & Rosswall, T. (1988). Microbial biomass as a fraction of potentially mineralizable nitrogen in soils from long-term field experiments. *Soil Biology & Biochemistry*, 20, 447–452.
- Brovelli, A., Batlle-Aguilar, J., & Barry, D. A. (2012). Analysis of carbon and nitrogen dynamics in riparian soils: Model development. *Science of the Total Environment*, 429, 231–245. <https://doi.org/10.1016/j.scitotenv.2012.04.027>
- Burke, I. C., Lauenroth, W. K., & Parton, W. J. (1997). Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology*, 78, 1330–1340. [https://doi.org/10.1890/0012-9658\(1997\)078\[1330:RATVIN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1330:RATVIN]2.0.CO;2)
- Butler, S. M., Melillo, J. M., Johnson, J. E., Mohan, J., Steudler, P. A., Lux, H., ... Bowles, F. (2012). Soil warming alters nitrogen cycling in a New England forest: Implications for ecosystem function and structure. *Oecologia*, 168, 819–828. <https://doi.org/10.1007/s00442-011-2133-7>
- Canfield, D. E., Glazer, A. N., & Falkowski, P. G. (2010). The evolution and future of earth's nitrogen cycle. *Science*, 330, 192–196. <https://doi.org/10.1126/science.1186120>
- Castro, H. F., Classen, A. T., Austin, E. E., Norby, R. J., & Schadt, C. W. (2010). Soil microbial community responses to multiple experimental climate change drivers. *Applied and Environmental Microbiology*, 76, 999–1007. <https://doi.org/10.1128/AEM.02874-09>
- Chambers, B. J., Lord, E. I., Nicholson, F. A., & Smith, K. A. (1999). Predicting nitrogen availability and losses following application of organic manures to arable land: MANNER. *Soil Use and Management*, 15, 137–143. <https://doi.org/10.1111/j.1475-2743.1999.tb00079.x>
- Colman, B. P., & Schimel, J. P. (2013). Drivers of microbial respiration and net N mineralization at the continental scale. *Soil Biology & Biochemistry*, 60, 65–76. <https://doi.org/10.1016/j.soilbio.2013.01.003>
- Curtin, D., Campbell, C. A., & Jalil, A. (1998). Effects of acidity on mineralization: pH-dependence of organic matter mineralization in weakly acidic soils. *Soil Biology & Biochemistry*, 30, 57–64. [https://doi.org/10.1016/S0038-0717\(97\)00094-1](https://doi.org/10.1016/S0038-0717(97)00094-1)
- Dawes, M. A., Schlegel, P., Hattenschwiler, S., Rixen, C., & Hagedorn, F. (2017). Soil warming opens the nitrogen cycle at the alpine treeline. *Global Change Biology*, 23, 421–434. <https://doi.org/10.1111/gcb.13365>
- Ekenler, M., & Tabatabai, M. A. (2002). Beta-glucosaminidase activity of soils: Effect of cropping systems and its relationship to nitrogen mineralization. *Biology and Fertility of Soils*, 36, 367–376.
- Erismann, J. W., Sutton, M. A., Galloway, J., Klimont, Z., & Winiwarter, W. (2008). How a century of ammonia synthesis changed the world. *Nature Geoscience*, 1, 636–639. <https://doi.org/10.1038/ngeo325>
- Fierer, N., & Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 626–631. <https://doi.org/10.1073/pnas.0507535103>
- Franzluebbers, A. J. (1999). Potential C and N mineralization and microbial biomass from intact and increasingly disturbed soils of varying texture. *Soil Biology & Biochemistry*, 31, 1083–1090. [https://doi.org/10.1016/S0038-0717\(99\)00022-X](https://doi.org/10.1016/S0038-0717(99)00022-X)
- Fraterrigo, J. M., Balser, T. C., & Turner, M. G. (2006). Microbial community variation and its relationship with nitrogen mineralization in historically altered forests. *Ecology*, 87, 570–579. <https://doi.org/10.1890/05-0638>
- Goyal, S., Mishra, M. M., Dhankar, S. S., Kapoor, K. K., & Batra, R. (1993). Microbial biomass turnover and enzyme-activities following the application of farmyard manure to field soils with and

- without previous long-term application. *Biology and Fertility of Soils*, 15, 60–64.
- Hassink, J. (1994). Effects of soil texture and grassland management on soil organic C and N and rates of C and N mineralization. *Soil Biology & Biochemistry*, 26, 1221–1231. [https://doi.org/10.1016/0038-0717\(94\)90147-3](https://doi.org/10.1016/0038-0717(94)90147-3)
- Hassink, J. (1995). Density fractions of soil macroorganic matter and microbial biomass as predictors of C-mineralization and N-mineralization. *Soil Biology & Biochemistry*, 27, 1099–1108.
- Hogberg, M. N., Chen, Y., & Hogberg, P. (2007). Gross nitrogen mineralisation and fungi-to-bacteria ratios are negatively correlated in boreal forests. *Biology and Fertility of Soils*, 44, 363–366. <https://doi.org/10.1007/s00374-007-0215-9>
- Jangid, K., Williams, M. A., Franzluebbers, A. J., et al. (2008). Relative impacts of land-use, management intensity and fertilization upon soil microbial community structure in agricultural systems. *Soil Biology & Biochemistry*, 40, 2843–2853. <https://doi.org/10.1016/j.soilbio.2008.07.030>
- Kallenbach, C., & Grandy, A. S. (2011). Controls over soil microbial biomass responses to carbon amendments in agricultural systems: A meta-analysis. *Agriculture Ecosystems & Environment*, 144, 241–252. <https://doi.org/10.1016/j.agee.2011.08.020>
- Kamimura, Y., & Hayano, K. (2000). Properties of protease extracted from tea-field soil. *Biology and Fertility of Soils*, 30, 351–355. <https://doi.org/10.1007/s003740050015>
- Kemmitt, S. J., Wright, D., Goulding, K. W. T., & Jones, D. L. (2006). pH regulation of carbon and nitrogen dynamics in two agricultural soils. *Soil Biology & Biochemistry*, 38, 898–911. <https://doi.org/10.1016/j.soilbio.2005.08.006>
- Keuper, F., Dorrepaal, E., Van Bodegom, P. M., Van Logtestijn, R., Venhuizen, G., Van Hal, J., & Aerts, R. (2017). Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species. *Global Change Biology*, 23, 4257–4266. <https://doi.org/10.1111/gcb.13804>
- Lee, K. H., & Jose, S. (2003). Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. *Forest Ecology and Management*, 185, 263–273. [https://doi.org/10.1016/S0378-1127\(03\)00164-6](https://doi.org/10.1016/S0378-1127(03)00164-6)
- Lefcheck, J. S. (2015). PiecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579.
- Lenth, R. V. (2018). *emmeans: Estimated Marginal Means, aka Least Squares Means*. R package version 1.1. Retrieved from <http://CRAN.R-project.org/package=emmeans>
- Liu, W., Zhang, Z., & Wan, S. (2009). Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Global Change Biology*, 15, 184–195. <https://doi.org/10.1111/j.1365-2486.2008.01728.x>
- Liu, Y., He, N., Wen, X., Yu, G., Gao, Y., & Jia, Y. (2016). Patterns and regulating mechanisms of soil nitrogen mineralization and temperature sensitivity in Chinese terrestrial ecosystems. *Agriculture Ecosystems & Environment*, 215, 40–46. <https://doi.org/10.1016/j.agee.2015.09.012>
- Liu, Y., Wang, C., He, N., Wen, X., Gao, Y., Li, S., ... Yu, G. (2017). A global synthesis of the rate and temperature sensitivity of soil nitrogen mineralization: Latitudinal patterns and mechanisms. *Global Change Biology*, 23, 455–464. <https://doi.org/10.1111/gcb.13372>
- Lober, R. W., & Reeder, J. D. (1993). Modified waterlogged incubation method for assessing nitrogen mineralization in soils and soil aggregates. *Soil Science Society of America Journal*, 57, 400–403. <https://doi.org/10.2136/sssaj1993.03615995005700020019x>
- Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., ... Li, B. (2013). Responses of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology*, 94, 726–738. <https://doi.org/10.1890/12-0279.1>
- McMillan, R., Quideau, S. A., Mackenzie, M. D., & Biryukova, O. (2007). Nitrogen mineralization and microbial activity in oil sands reclaimed boreal forest soils. *Journal of Environmental Quality*, 36, 1470–1478. <https://doi.org/10.2134/jeq2006.0530>
- Mikha, M. M., Rice, C. W., & Milliken, G. A. (2005). Carbon and nitrogen mineralization as affected by drying and wetting cycles. *Soil Biology & Biochemistry*, 37, 339–347. <https://doi.org/10.1016/j.soilbio.2004.08.003>
- Nasholm, T., Ekblad, A., Nordin, A., Giesler, R., Hogberg, M., & Hogberg, P. (1998). Boreal forest plants take up organic nitrogen. *Nature*, 392, 914–916. <https://doi.org/10.1038/31921>
- Nayak, D. R., Babu, Y. J., & Adhya, T. K. (2007). Long-term application of compost influences microbial biomass and enzyme activities in a tropical Aeric Endoaquept planted to rice under flooded condition. *Soil Biology & Biochemistry*, 39, 1897–1906. <https://doi.org/10.1016/j.soilbio.2007.02.003>
- Niu, S., Classen, A. T., Dukes, J. S., Kardol, P., Liu, L., Luo, Y., ... Zaehle, S. (2016). Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle. *Ecology Letters*, 19, 697–709.
- Osterholz, W. R., Rinot, O., Shaviv, A., Linker, R., Liebman, M., Sanford, G., ... Castellano, M. J. (2017). Predicting gross nitrogen mineralization and potentially mineralizable nitrogen using soil organic matter properties. *Soil Science Society of America Journal*, 81, 1115–1126. <https://doi.org/10.2136/sssaj2017.02.0055>
- Pathak, H., & Rao, D. L. N. (1998). Carbon and nitrogen mineralization from added organic matter in saline and alkali soils. *Soil Biology & Biochemistry*, 30, 695–702. [https://doi.org/10.1016/S0038-0717\(97\)00208-3](https://doi.org/10.1016/S0038-0717(97)00208-3)
- Pennanen, T., Fritze, H., Vanhala, P., Kiikkila, O., Neuvonen, S., & Baath, E. (1998). Structure of a microbial community in soil after prolonged addition of low levels of simulated acid rain. *Applied and Environmental Microbiology*, 64, 2173–2180.
- Pietri, J. C. A., & Brookes, P. C. (2008). Relationships between soil pH and microbial properties in a UK arable soil. *Soil Biology & Biochemistry*, 40, 1856–1861. <https://doi.org/10.1016/j.soilbio.2008.03.020>
- Rousk, J., Brookes, P. C., & Baath, E. (2009). Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology*, 75, 1589–1596. <https://doi.org/10.1128/AEM.02775-08>
- Rousk, K., Michelsen, A., & Rousk, J. (2016). Microbial control of soil organic matter mineralization responses to labile carbon in subarctic climate change treatments. *Global Change Biology*, 22, 4150–4161. <https://doi.org/10.1111/gcb.13296>
- Rustad, L. E., Campbell, J. L., Marion, G. M., et al. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126, 543–562. <https://doi.org/10.1007/s004420000544>
- Schimel, J. P., & Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing paradigm. *Ecology*, 85, 591–602. <https://doi.org/10.1890/03-8002>
- Schulten, H. R., & Schnitzer, M. (1997). The chemistry of soil organic nitrogen: A review. *Biology and Fertility of Soils*, 26, 1–15. <https://doi.org/10.1007/s003740050335>
- Serna-Chavez, H. M., Fierer, N., & Vanbodegom, P. M. (2013). Global drivers and patterns of microbial abundance in soil. *Global Ecology and Biogeography*, 22, 1162–1172. <https://doi.org/10.1111/geb.12070>
- Singh, R., & Nye, P. H. (1984). The effect of soil pH and high urea concentrations on urease activity in soil. *Journal of Soil Science*, 35, 519–527. <https://doi.org/10.1111/j.1365-2389.1984.tb00609.x>
- Sinsabaugh, R. L., Lauber, C. L., Weintraub, M. N., Ahmed, B., Allison, S. D., Crenshaw, C., ... Zeglin, L. H. (2008). Stoichiometry of soil enzyme activity at global scale. *Ecology Letters*, 11, 1252–1264. <https://doi.org/10.1111/j.1461-0248.2008.01245.x>
- Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N. S., Wijesundera, R., ... Abarenkov, K. (2014). Global diversity and geography of soil fungi. *Science*, 346, 1078. <https://doi.org/10.1126/science.1256688>

- Thornton, P. E., Doney, S. C., Lindsay, K., Moore, J. K., Mahowald, N., Randerson, J. T., ... Lee, Y.-H. (2009). Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: Results from an atmosphere-ocean general circulation model. *Biogeosciences*, 6, 2099–2120. <https://doi.org/10.5194/bg-6-2099-2009>
- Thornton, P. E., Lamarque, J.-F., Rosenbloom, N. A., & Mahowald, N. M. (2007). Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability. *Global Biogeochemical Cycles*, 21, GB4018.
- Treseder, K. K. (2008). Nitrogen additions and microbial biomass: A meta-analysis of ecosystem studies. *Ecology Letters*, 11, 1111–1120. <https://doi.org/10.1111/j.1461-0248.2008.01230.x>
- Verhoef, H. A., & Brussaard, L. (1990). Decomposition and nitrogen mineralization in natural and agroecosystems – the contribution of soil animals. *Biogeochemistry*, 11, 175–211.
- Von Bloh, W., Schaphoff, S., Mueller, C., Rolinski, S., Waha, K., & Zaehle, S. (2018). Implementing the nitrogen cycle into the dynamic global vegetation, hydrology, and crop growth model LPJmL (version 5.0). *Geoscientific Model Development*, 11, 2789–2812. <https://doi.org/10.5194/gmd-11-2789-2018>
- Wang, W. J., Chalk, P. M., Chen, D., & Smith, C. J. (2001). Nitrogen mineralisation, immobilisation and loss, and their role in determining differences in net nitrogen production during waterlogged and aerobic incubation of soils. *Soil Biology & Biochemistry*, 33, 1305–1315. [https://doi.org/10.1016/S0038-0717\(01\)00034-7](https://doi.org/10.1016/S0038-0717(01)00034-7)
- Wieder, W. R., Bonan, G. B., & Allison, S. D. (2013). Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change*, 3, 909–912. <https://doi.org/10.1038/nclimate1951>
- Xu, X., Schimel, J. P., Janssens, I. A., et al. (2017). Global pattern and controls of soil microbial metabolic quotient. *Ecological Monographs*, 87, 429–441. <https://doi.org/10.1002/ecm.1258>
- Xu, X., Thornton, P. E., & Post, W. M. (2013). A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography*, 22, 737–749. <https://doi.org/10.1111/geb.12029>
- Zaehle, S., Friend, A. D., Friedlingstein, P., Dentener, F., Peylin, P., & Schulz, M. (2010). Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance. *Global Biogeochemical Cycles*, 24, GB1006.

SUPPORTING INFORMATION

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

How to cite this article: Li Z, Tian D, Wang B, et al. Microbes drive global soil nitrogen mineralization and availability. *Glob Change Biol*. 2019;25:1078–1088. <https://doi.org/10.1111/gcb.14557>