

Global patterns and controlling factors of soil nitrification rate

Zhaolei Li^{1,2,3} | Zhaoqi Zeng^{1,4} | Dashuan Tian¹  | Jinsong Wang¹  | Zheng Fu¹ | Fangyue Zhang¹ | Ruiyang Zhang¹ | Weinan Chen^{1,4} | Yiqi Luo³  | Shuli Niu^{1,4} 

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

²National Engineering Laboratory for Efficient Utilization of Soil and Fertilizer Resources, Key Laboratory of Agricultural Environment in Universities of Shandong, College of Resources and Environment, Shandong Agricultural University, Taian, PR China

³Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA

⁴College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, PR 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 100101, PR China.
Email: sniu@igsnr.ac.cn

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Abstract

Soil nitrification, an important pathway of nitrogen transformation in ecosystems, produces soil nitrate that influences net primary productivity, while the by-product of nitrification, nitrous oxide, is a significant greenhouse gas. Although there have been many studies addressing the microbiology, physiology, and impacting environment factors of soil nitrification at local scales, there are very few studies on soil nitrification rate over large scales. We conducted a global synthesis on the patterns and controlling factors of soil nitrification rate normalized at 25°C by compiling 3,140 observations from 186 published articles across terrestrial ecosystems. Soil nitrification rate tended to decrease with increasing latitude, especially in the Northern Hemisphere, and varied largely with ecosystem types. The soil nitrification rate significantly increased with mean annual temperature (MAT), soil nitrogen content, microbial biomass carbon and nitrogen, soil ammonium, and soil pH, but decreased with soil carbon:nitrogen and carbon:nitrogen of microbial biomass. The total soil nitrogen content contributed the most to the variations of global soil nitrification rate (total coefficient = 0.29) in structural equation models. The microbial biomass nitrogen (MBN; total coefficient = 0.19) was nearly of equivalent importance relative to MAT (total coefficient = 0.25) and soil pH (total coefficient = 0.24) in determining soil nitrification rate, while soil nitrogen and pH influenced soil nitrification via changing soil MBN. Moreover, the emission of soil nitrous oxide was positively related to soil nitrification rate at a global scale. This synthesis will advance our current understanding on the mechanisms underlying large-scale variations of soil nitrification and benefit the biogeochemical models in simulating global nitrogen cycling.

KEYWORDS

climate, microbial biomass, nitrogen cycle, soil nitrification rate, soil pH

1 | INTRODUCTION

Soil nitrification, the oxidation of ammonium to nitrate, is a crucial process in nitrogen cycling. The annual cycle of nitrogen via global soil nitrification was estimated at 330 Tg nitrate/year, which is next only to the nitrogen mineralization on Earth (Kuypers, Marchant, & Kartal, 2018). Soil nitrification can produce nitrous oxide that is

a potent greenhouse gas, and the product of soil nitrification, soil nitrate, is one important form of the available nitrogen for plant growth. Thus, it is important for terrestrial net primary production (Wieder, Cleveland, Smith, & Todd-Brown, 2015). Soil nitrification is changed under global change (Barnard, Leadley, & Hungate, 2005), which can alter soil nitrogen availability and nitrous oxide emission. A recent study reports a decrease of soil nitrogen availability from

1973 to 2011 that may be partially due to the reduction of nitrification rate (Duran et al., 2016). Thus, accurately predicting soil nitrification is very helpful to better understand the dynamics of soil available nitrogen (Norton & Ouyang, 2019) and nitrous oxide emission. However, many models, e.g., CENTURY model (Cannavo, Recous, Parnaudeau, & Reau, 2008), cannot simulate soil nitrification rate well since regulators of soil nitrification are not yet well understood at large scales although many case studies have been conducted at the local scale. Thus, it is imperative to reveal the patterns of soil nitrification rate and its controlling factors at a global scale.

Soil nitrification can be influenced by climatic factors, soil properties, and microbial characteristics. While soil nitrification is expected to be influenced by temperature, no consistent patterns have been found. Some studies reveal that global warming slightly decreases soil nitrification rate (7%; Gao & Yan, 2019), whereas other studies find that warming substantially increases nitrification rate (54%; Bork, Attaeianb, Cahillc, & Changd, 2019). Precipitation can change the emission of nitrous oxide as well as the content of nitrate (Gu & Riley, 2010), indicating that soil nitrification is mediated by precipitation. Soil pH can regulate soil nitrification as well. The added anhydrous ammonia nitrifies 89% with soil pH > 7.5, whereas it only nitrifies 39% with soil pH < 6.0 (Kyveryga, Blackmer, Ellsworth, & Isla, 2004). Additionally, increases in soil pH by soil liming stimulate soil nitrifying activity (Nugroho, Roling, Laverman, & Verhoef, 2007). The substrate can also significantly impact soil nitrification. The higher contents of soil ammonium are conventionally assumed to lead to higher soil nitrification rate (Zhao, Cai, & Xu, 2007); however, some studies find that the addition of ammonia into soil does not increase soil nitrification rate (Flowers & Ocallaghan, 1983). Furthermore, the results of isotope tracking approach show that the added soil ammonia is mostly immobilized and the nitrifying activity does not relate apparently to fertilizer applications (Bengtsson & Bergwall, 2000). Soil organic nitrogen provides substrates for heterotrophic nitrification that is also an important nitrification pathway (Schimel, Firestone, & Killham, 1984). Heterotrophic nitrification accounts for 7%–19% of total nitrification in grasslands (Islam, Chen, & White, 2007), and even accounts for 69% of the nitrate produced in acid cropping soil (Liu, Suter, He, Hayden, & Chen, 2015). Bacteria (Brierley & Wood, 2001) and fungi (Lang & Jagnow, 1986) are the participants of soil heterotrophic nitrification, and ammonia-oxidizing bacteria and ammonia-oxidizing archaea are participants of autotrophic nitrification (Martens-Habbena, Berube, Urakawa, de la Torre, & Stahl, 2009). Thus, microorganisms may play an important role in soil nitrification. Although these impacting factors have been individually evaluated, it is hard to comprehensively understand soil nitrification unless the relative roles of climatic factors, soil properties, and microbial characteristics in nitrification are clarified.

Nitrification includes autotrophic nitrification and heterotrophic nitrification. The substrate of autotrophic nitrification is ammonium that comes from nitrogen mineralization of soil organic nitrogen and

fertilizer applied by humans. The substrates of heterotrophic nitrification are soil organic nitrogen. Therefore, total soil nitrogen (TN; mostly in organic forms) can influence both autotrophic nitrification and heterotrophic nitrification, while soil ammonium only impacts autotrophic nitrification. We hypothesized that the content of TN was a more important factor driving the variations of global soil nitrification compared to soil ammonium (H1). Soil nitrification is mainly performed by microorganisms that are sensitive to environmental change (Wang, Angle, Chaney, Delorme, & McIntosh, 2006). Thus, climatic factors and/or soil properties may indirectly influence soil nitrification through changing soil microbial biomass nitrogen (MBN) at large spatial scales (H2).

Nitrous oxide, a by-product of soil nitrification, is a potent greenhouse gas in the atmosphere. While the emission of soil nitrous oxide has increased up to 10.0 ± 2.0 Tg/year, large uncertainties exist in projection of the soil nitrous oxide emission (Tian et al., 2019). To reduce this uncertainty, many studies have been conducted to identify the underlying mechanisms, mainly from processes related to climatic factors and microbial diversity (Butterbach-Bahl, Baggs, Dannenmann, Kiese, & Zechmeister-Boltenstern, 2013). However, modeling based on soil nitrification processes may offer an alternative but mechanistic approach to predict the emission of nitrous oxide from ecosystem processes. Indeed, Szukics et al. (2010) have revealed that the emission of soil nitrous oxide is positively correlated with nitrification rate in forest ecosystem. Maag and Vinther (1996) reported that higher soil nitrification leads to higher nitrous oxide emission across the five soil types. However, previous studies have only revealed site-specific patterns. It remains to be explored whether and how soil nitrification determines the emissions of soil nitrous oxide at a global scale.

This study was designed to reveal global patterns of soil nitrification rates and controlling factors. Specifically, we compiled 3,140 observations from 186 published articles to address three questions: (a) What would the global pattern be for soil nitrification rates? (b) How do climatic factors, soil properties, and microbial characteristics relatively influence global soil nitrification rate? (c) How is the emission of soil nitrous oxide associated with soil nitrification rates at a global scale?

2 | MATERIALS AND METHODS

2.1 | Data compilation and overview

The dataset of soil nitrification was constructed by compiling data from published peer-viewed articles. Initially, we screened articles using the key terms, "soil nitrification" OR "nitrogen nitrification", in the China National Knowledge Infrastructure Database (<http://www.cnki.net>) and Web of Science (<http://apps.webofknowledge.com>) up to 30 May 2019. Subsequently, we sifted the database of screened articles to remove duplicates, resulting in 916 articles. The criteria for collecting eligible data of soil nitrification were: (a) soil nitrification was measured using the upper soil sample (mostly to

the top 20 cm soil depth); (b) soil nitrification was measured when incubations (the majority came from laboratory incubation) took longer than 48 hr to eliminate the effects of disturbance; (c) the conditions of soil incubation were available. There were 186 articles matching these criteria.

We also extracted the geographic coordinates (latitude and longitude), climatic factors (mean annual temperature [MAT] and mean annual precipitation [MAP]), soil properties (the content of soil sand and clay, soil pH, the content of soil organic carbon, TN, and the ratio of soil carbon to nitrogen [C:N]), available nutrients (the content of soil ammonium and soil available phosphorus [AP]), and the characteristics of soil microbial biomass (microbial biomass carbon [MBC], MBN, and the ratio of microbial biomass carbon to microbial biomass nitrogen). In addition, we collected the data on soil nitrate concentrations before soil incubation and the emission of nitrous oxide from articles. Meanwhile, replicates of soil incubation were also extracted from original articles.

The constructed dataset of soil nitrification included 3,140 observations from 186 studies. The types of terrestrial ecosystem in this dataset included croplands (1,423 observations), forests (841 observations), grasslands (368 observations), wetlands (80 observations), and unclassified ecosystems (428 observations). The dataset covered all continents but Antarctica, however, the data were mainly from Asia (1,682 observations), North America (443 observations), and Europe (323 observations).

2.2 | Data analyses

There were several incubation temperatures ranging from 25 to 35°C, however, most soil nitrification rates were measured at 25°C (1,598 in 3,140 observations). We adjusted all soil nitrification rates to 25°C using $Q_{10} = 2$ according to Formula (1),

$$\text{Nitrification}_2 / \text{Nitrification}_1 = Q_{10}^{(25 - T_1) / 10}, \quad (1)$$

where Nitrification_1 and Nitrification_2 are the original soil nitrification rate and adjusted nitrification rate (i.e., potential nitrification rate), respectively. T_1 is the incubated temperature for Nitrification_1 .

The latitudinal pattern of soil nitrification was tested using a linear mixed-effect model. The relationships of soil nitrification with climatic factors, soil properties, and the characteristics of microbial biomass were also examined using a linear mixed-effect model. The linear mixed-effect model is

$$\ln(\text{Nitrification}_2) = \beta_0 + \beta_1 \times \ln X + \pi_{\text{study}} + \varepsilon, \quad (2)$$

where β_0 , β_1 , π_{study} and ε are the intercept, slope value, the random effect, and sampling error, and $\ln X$ refers to environmental factors, respectively. The “study” was viewed as a random effect that could consider the autocorrelation among observations within the same article. The relationships between the content of soil nitrate/the emission of

nitrous oxide and soil nitrification rate were also tested using a linear mixed-effect model. The linear mixed-effect model is

$$\ln Y = \beta_0 + \beta_1 \times \ln(\text{Nitrification}_2) + \pi_{\text{study}} + \varepsilon, \quad (3)$$

where Y is the content of soil nitrate or the emission of nitrous oxide. We calculated the average soil nitrification of each ecosystem (e.g., croplands, forests, grasslands, and wetlands), and comparison of soil nitrification across ecosystems was performed with Tukey HSD test using the “stats” package.

Finally, the multivariable relationships between soil nitrification rate and environmental factors were tested using structural equation models. The conceptual structural equation models contained the direct relationships between soil nitrification and climate, soil properties, and the characteristics of microbial biomass, as well as the indirect effects that the climate and/or soil properties influenced soil nitrification via changing microbial biomass. Likewise, multivariable relationships between the contents of soil nitrate and environmental factors were also tested in structural equation models. In structural equation models, the environmental factors were treated as the fixed effects, the “study” was viewed as the random effect, and the replicates were regarded as “weight”. The optimal structural equation model with the minimum Akaike information criterion value was presented here ($AIC = 55$, $p = .32$). In the optimal model the redundant environmental factors were removed, such as the soil texture and the concentrations of AP. Testing of structure equation models was performed using *piecewiseSEM* package (Lefcheck, 2016).

3 | RESULTS

3.1 | Changes of soil nitrification rate with latitude, ecosystem types, and climate zones

Soil nitrification rate tended to decrease from low latitude to high latitude with a slope of -0.006 (the nitrification was logarithmically transformed; Figure 1a). The global mean soil nitrification rate was $3.20 \text{ mg kg}^{-1} \text{ day}^{-1}$ ($SE = 0.094$, $N = 3,140$; Figure 1b). The mean soil nitrification rate was $3.82 \text{ mg kg}^{-1} \text{ day}^{-1}$ ($SE = 0.151$, $N = 1,423$) in croplands, which was greater than those of forests ($2.58 \text{ mg kg}^{-1} \text{ day}^{-1}$, $SE = 0.153$, $N = 841$) and grasslands ($1.70 \text{ mg kg}^{-1} \text{ day}^{-1}$, $SE = 0.117$, $N = 368$), but there were no significant differences in soil nitrification rate between croplands and wetlands ($3.29 \text{ mg kg}^{-1} \text{ day}^{-1}$, $SE = 0.702$, $N = 80$). Among natural ecosystems, soil nitrification rate was the least in grasslands. The average soil nitrification rate was greatest under tropical climate ($6.29 \pm 0.237 \text{ mg kg}^{-1} \text{ day}^{-1}$; Figure 1c) and the average soil nitrification rates were least under humid continent climate ($1.82 \pm 0.135 \text{ mg kg}^{-1} \text{ day}^{-1}$), hot desert climate ($1.83 \pm 0.095 \text{ mg kg}^{-1} \text{ day}^{-1}$), and cold semiarid climate ($1.68 \pm 0.078 \text{ mg kg}^{-1} \text{ day}^{-1}$).

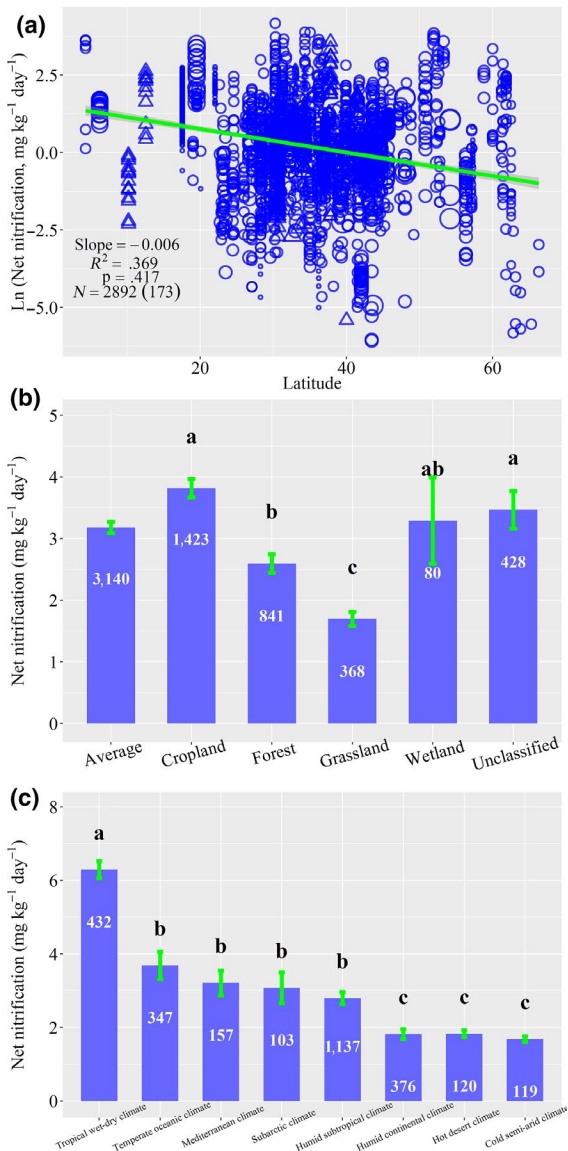


FIGURE 1 The changes of soil nitrification rate with latitude (a), ecosystems (b), and climate zones (c). The green line and the gray shades stand for the slope and 95% confidence intervals, respectively (a). The circles come from North Hemisphere, while the triangles come from South Hemisphere. The size of dots refers to the replicates ranging from 1 to 30. The green bars represent the standard error and the white values are the numbers of observations in ecosystems (b and c). The climate zones have been classified according to Köppen Climate Classification. Mediterranean climate includes Hot-summer Mediterranean climate and Warm-summer Mediterranean climate. Subarctic climate includes Monsoon-influenced Subarctic climate. Humid Subtropical climate includes Monsoon-influenced humid Subtropical climate. Humid Continental climate includes Hot-summer Humid Continental climate, Warm-summer Humid Continental climate, and Monsoon-influenced Warm-summer humid Continental climate. The average soil nitrification rate of climate zone with the observations being more than 100 is presented (c). The different letters above bars indicate significantly different soil nitrification rates among ecosystems (b) or climate zones (c). The significance level was set at <.05 [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Bivariate relationships of soil nitrification rate with climate, soil properties, and microbial biomass

Soil nitrification rate significantly increased with MAT with a slope of 0.684 at a global scale ($p < .001$; Figure 2a), and the relationship was robust using the data excluding the observations with the lowest MAT (slope = 0.744, $p < .001$; Figure S1). Soil nitrification rate slightly decreased with MAP with a slope of -0.270 ($p = .040$; Figure 2b) at a global scale.

Of the soil properties, soil nitrification rate significantly increased with soil pH at a global scale with a slope of 0.314 ($p < .001$; Figure 3a).

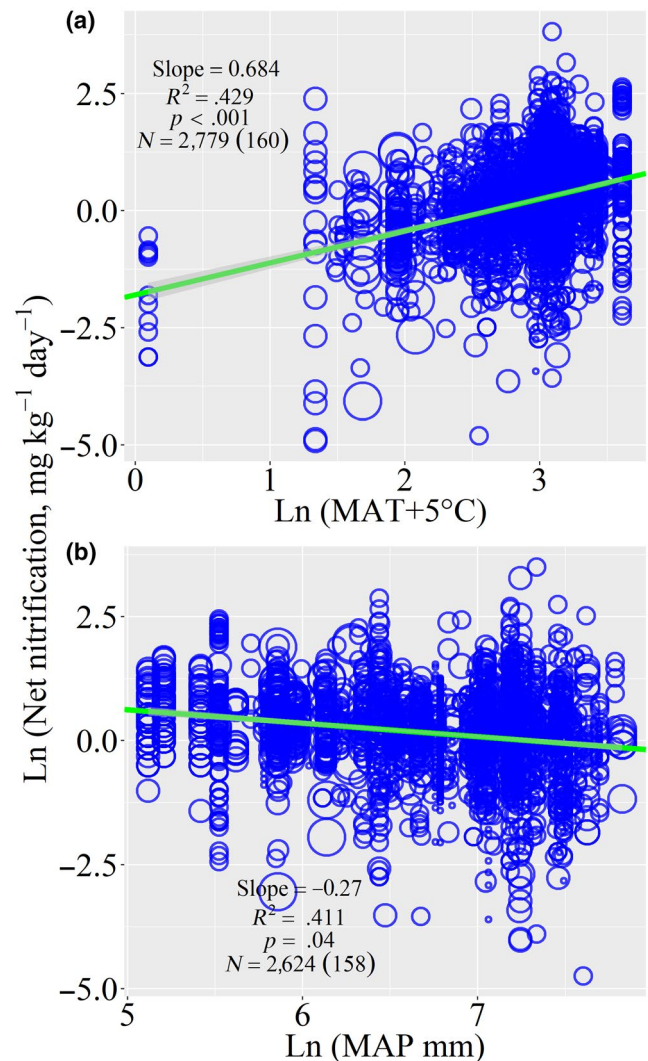


FIGURE 2 The bivariate relationships between soil nitrification rate and climatic factors, namely, mean annual temperature (MAT, a) and mean annual precipitation (MAP, b) at a global scale using the logarithmically transformed data. The green lines represent slopes from the linear mixed effects models and the gray shadings are the 95% confidence intervals. The size of circles is the number of replicates from 1 to 30. The figure without parentheses denotes the number of observations and the figure in parentheses denotes the number of studies [Colour figure can be viewed at wileyonlinelibrary.com]

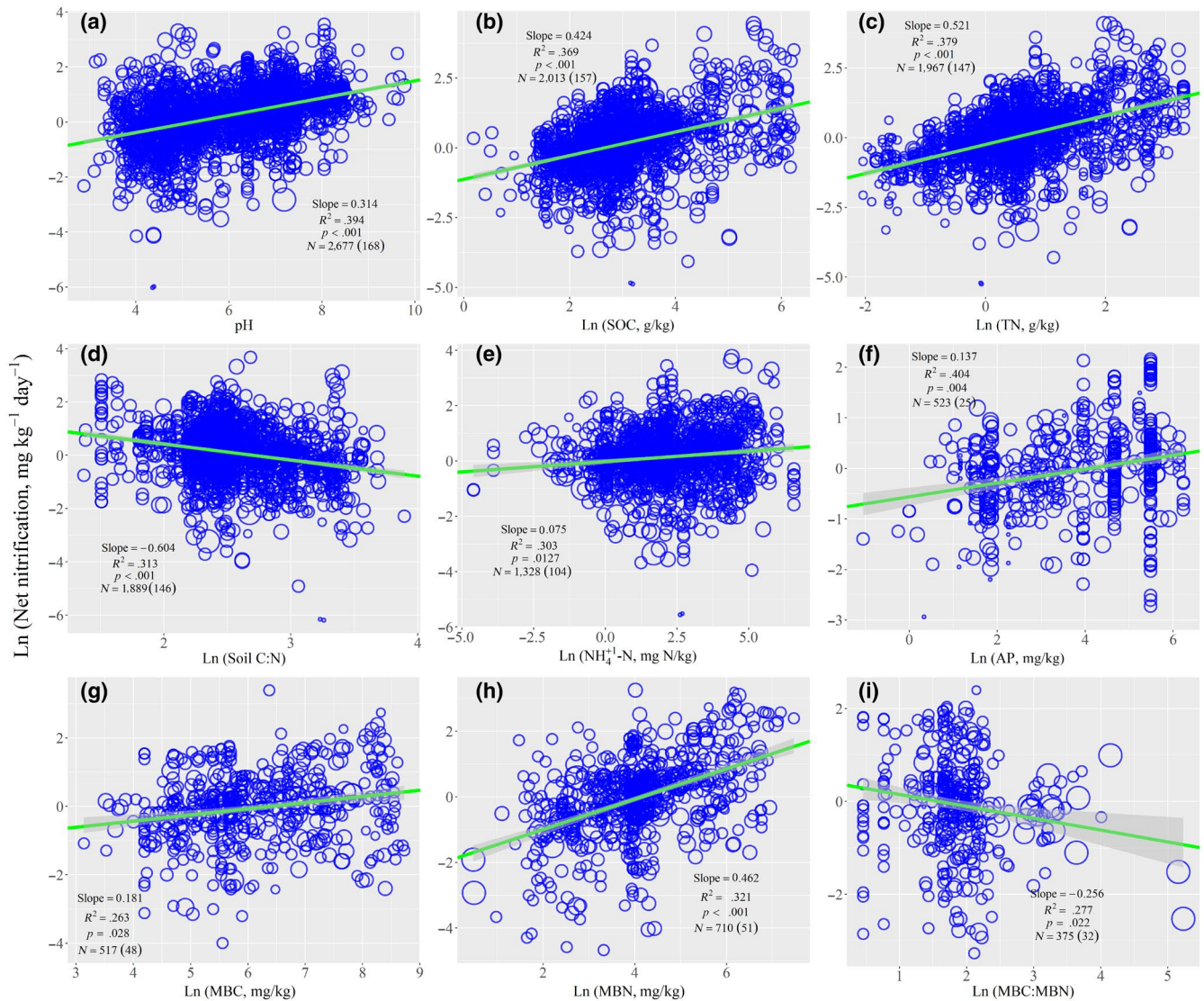


FIGURE 3 The bivariate relationships between soil nitrification rate and soil properties, namely, soil pH (a), the content of soil organic carbon (SOC, b), the content of soil nitrogen (TN, c), the ratio of soil carbon to nitrogen (soil C:N, d), the content of soil ammonium (e), the content of available phosphorus (AP, f), microbial biomass carbon (MBC, g), microbial biomass nitrogen (MBN, h), and the ratio of microbial biomass carbon to microbial biomass nitrogen (MBC:MBN, i) at a global scale using logarithmically transformed data. The green lines are the slopes from the linear mixed effects models and the gray shadings are the 95% confidence intervals. The size of circles is the number of replicates from 1 to 30. The number without parentheses is the amount of observations and the number with parentheses is the amount of studies [Colour figure can be viewed at wileyonlinelibrary.com]

Moreover, soil nitrification rate was significantly related to the content of soil organic carbon, TN, and the C:N. Specifically, soil nitrification rate increased with the content of soil organic carbon ($p < .001$; Figure 3b) and TN ($p < .001$; Figure 3c), whereas the soil nitrification rate decreased with the C:N ($p < .001$; Figure 3d). Additionally, soil nitrification rate slightly increased with the content of soil ammonium ($p = .013$; Figure 3e) and the AP at a global scale ($p = .004$; Figure 3f). There were no significant relationships between soil nitrification rate and soil texture (Figure S2).

Soil nitrification rate was correlated significantly with the characteristics of microbial biomass (Figure 3g–i). Specifically, soil nitrification rate increased with the content of soil MBC (slope = 0.181, $p = .028$) and MBN (slope = 0.462, $p < .001$) at the global scale. Soil

nitrification rate decreased with higher ratio of soil microbial biomass carbon to microbial biomass nitrogen (slope = -0.256 , $p = .022$).

For different ecosystem types, soil nitrification rate significantly increased with total nitrogen content in croplands (slope = 0.33, $p < .001$; Figure 4), forests (slope = 0.75, $p < .001$), and wetland (slope = 0.34, $p = .05$), while nitrification rate tended to increase with soil total nitrogen in grasslands (slope = 0.38, $p = .10$). Moreover, soil nitrification rate significantly increased with soil MBN in croplands (slope = 0.30, $p = .001$) and forests (slope = 0.68, $p < .001$). In addition, soil nitrification rates were influenced by climatic factors and soil properties in each ecosystem. For example, soil nitrification rates were greater under higher MAT, particularly in forests (slope = 0.42, $p = .004$) and grasslands (slope = 0.58, $p < .001$). Soil nitrification

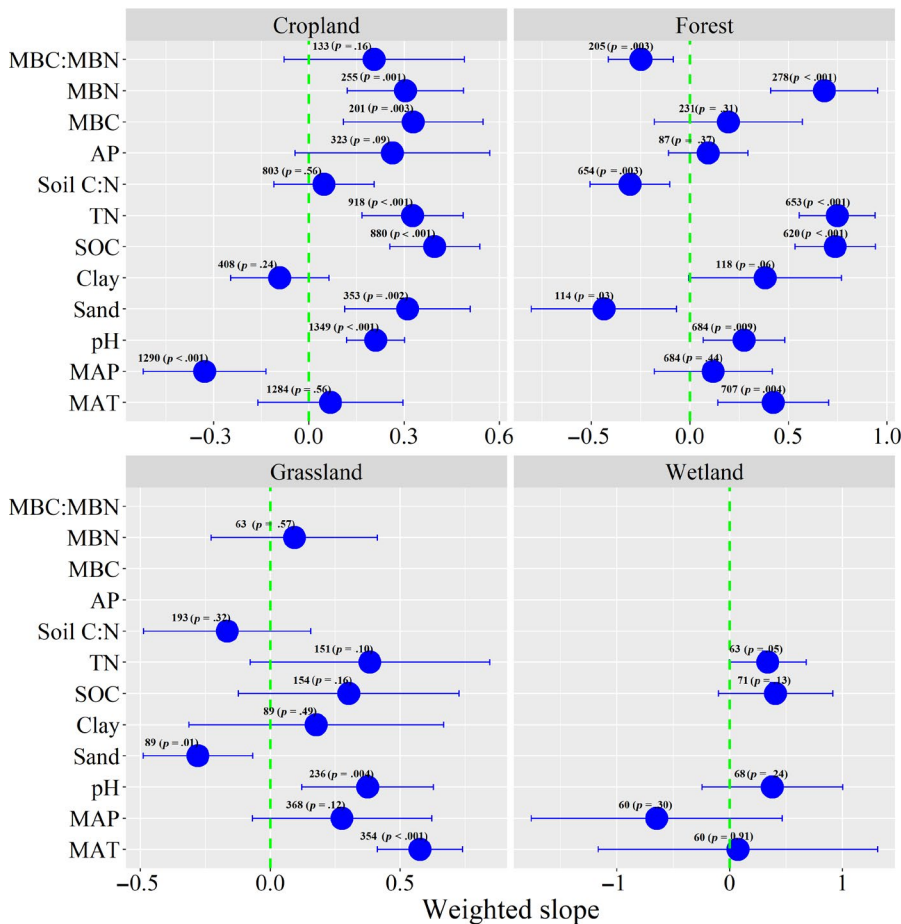


FIGURE 4 The slopes of the bivariate relationships between soil nitrification rate and MAT, MAP, pH, Sand, Clay, SOC, TN, soil C:N, AP, MBC, MBN, and MBC:MBN across ecosystems. The blue dot represents the mean \pm 95% confidence intervals of the slope between soil nitrification rate and variable. The values in parentheses are the p values and values without parentheses are the number of observations. MAT, MAP, SOC, TN, soil C:N, AP, MBC, MBN, and MBC:MBN represent mean annual temperature, mean annual precipitation, total soil organic carbon, total soil nitrogen, the ratio of soil carbon to nitrogen, soil available phosphorus, soil microbial biomass carbon, microbial biomass nitrogen, and carbon: nitrogen ratio of soil microbial biomass, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

rates significantly and positively correlated with soil pH in croplands (slope = 0.21, $p < .001$), forests (slope = 0.28, $p = .009$), and grasslands (slope = 0.38, $p = .004$).

3.3 | Multivariable relationships between soil nitrification rate and environmental factors

The multivariable relationship analysis showed that the important controlling factors for the global variations of soil nitrification rate were MAT, TN, soil pH, MBN, and the C:N (Figure 5). Soil nitrification rate correlated positively with MAT (standardized coefficient = 0.25, $p < .001$), TN (standardized coefficient = 0.24, $p < .001$), soil pH (standardized coefficient = 0.22, $p < .001$), and MBN (standardized coefficient = 0.19, $p < .001$), whereas soil nitrification rate correlated negatively with the C:N (standardized coefficient = -0.10 , $p < .001$). The pivotal driving factor on soil nitrification rate was the content of TN in combination with direct and indirect effects at a global scale (total coefficient = 0.293). The second important driving factors on soil nitrification were MAT (total coefficient = 0.250) and soil pH (total coefficient = 0.241). The climate and soil properties could influence soil nitrification rate via MBN. For instance, the MAP promoted the nitrification rate by increasing MBN (standardized coefficient = 0.017, $p = .048$). Similarly, TN and soil pH also influenced nitrification by increasing the MBN (standardized coefficient = 0.053,

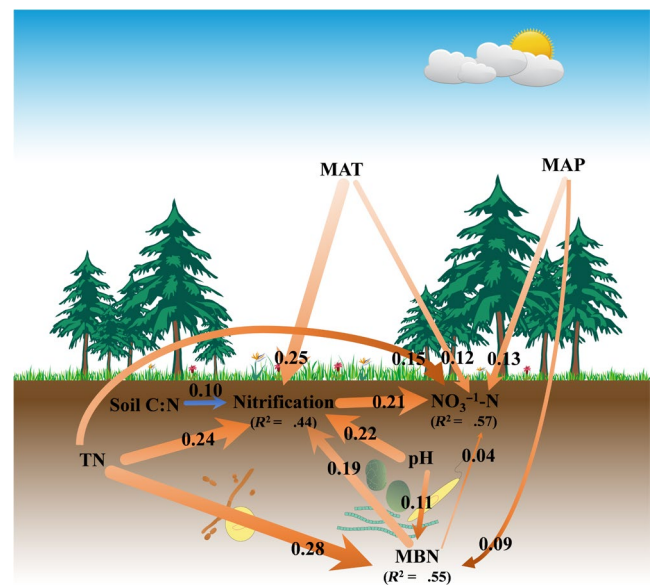


FIGURE 5 The multiple relationships of soil nitrification rate at the global scale. The orange lines are the significantly positive relationships, and blue lines are the significantly negative relationships, in which the statistically significant level is $\alpha \leq 0.05$. Numbers beside arrows are standardized coefficients. MAT, MAP, TN, soil C:N, and MBN represent mean annual temperature, mean annual precipitation, total soil nitrogen, the ratio of soil carbon to nitrogen, and microbial biomass nitrogen, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

$p < .001$; standardized coefficient = 0.021, $p < .001$, respectively). The environmental factors in combination accounted for the 44% of variations in global soil nitrification rate.

3.4 | Relationships between soil nitrification rate and soil nitrate contents and nitrous oxide emissions

The contents of soil nitrate significantly increased with the higher soil nitrification rate with a slope of 0.325 ($p < .001$; Figure 6a). Although MAT (standardized coefficient = 0.12, $p = .008$), MAP (standardized coefficient = 0.13, $p = .004$), TN (standardized coefficient = 0.15,

$p < .001$), and MBN (standardized coefficient = 0.04, $p = .032$) influenced the contents of soil nitrate, the most important factor driving the variations of global soil nitrate was soil nitrification rate (standardized coefficient = 0.21, $p < .001$; Figure 5). Moreover, the emissions of nitrous oxide related significantly to soil nitrification rate at a global scale, because there was positive relationship between the emissions of nitrous oxide and the soil nitrification rate with a slope of 0.441 ($p < .001$).

4 | DISCUSSION

This study reveals the large-scale variations of soil nitrification rate across ecosystems and climate types, and quantifies controlling factors of soil nitrification rate at a global scale. Although there have been many studies estimating soil nitrification rate and exploring its influencing factors, there are very few estimates of soil nitrification over large scales. The main finding of this synthesis that soil nitrogen substrates (e.g., soil total nitrogen) and microbial biomass mainly control the variations of soil nitrification rate implies that the incorporation of soil nitrogen substrates and microbial biomass characteristics into current nitrogen cycling model will improve the prediction of soil nitrification and global nitrogen cycling.

4.1 | Controlling factors for the global variations of soil nitrification rate

Total soil nitrogen content, MAT, soil pH, and MBN were the key controlling factors of soil nitrification rate at the global scale. Among them, total soil nitrogen content is the most important determinant, which may be due to the following mechanisms. First, the amount of global TN, which mostly constitutes of organic nitrogen, is estimated as 133–140 Pg in the upper 100 cm soil (Batjes, 1996). This provides substantial substrate for soil nitrogen mineralization and nitrification. Previous studies reported that soil with higher organic nitrogen possesses greater net soil nitrification (Yao, Campbell, & Qiao, 2011; Zaman & Chang, 2004). Second, soil with high total nitrogen usually has high MBN at ecosystem and regional scales (Shibahara & Inubushi, 1997; Yang, Zhu, Zhang, Yan, & Sun, 2010). Third, the activity of nitrification microorganisms is usually stimulated by nitrogen availability. *amoA*, a functional gene of nitrification microorganisms, increases with urea fertilization (Lu et al., 2012). Tong and Xu (2012) also reveal that urea additions stimulate ammonia-oxidizing bacteria and thus accelerate nitrification. The soil nitrifying enzyme activities positively correlate with the content of soil organic matter, particularly in clayey soils (Silva, Poly, Guillaumaud, van Elsas, & Salles, 2012).

Recent research has shown that the amount of heterotrophic nitrification is considerable in acidic soil and estimated to contribute to more than 60% of total soil nitrification (Zhang, Wang, Zhong, & Cai, 2015). The ammonium from the organic nitrogen decomposition is the substrate of soil autotrophic nitrification, and a previous

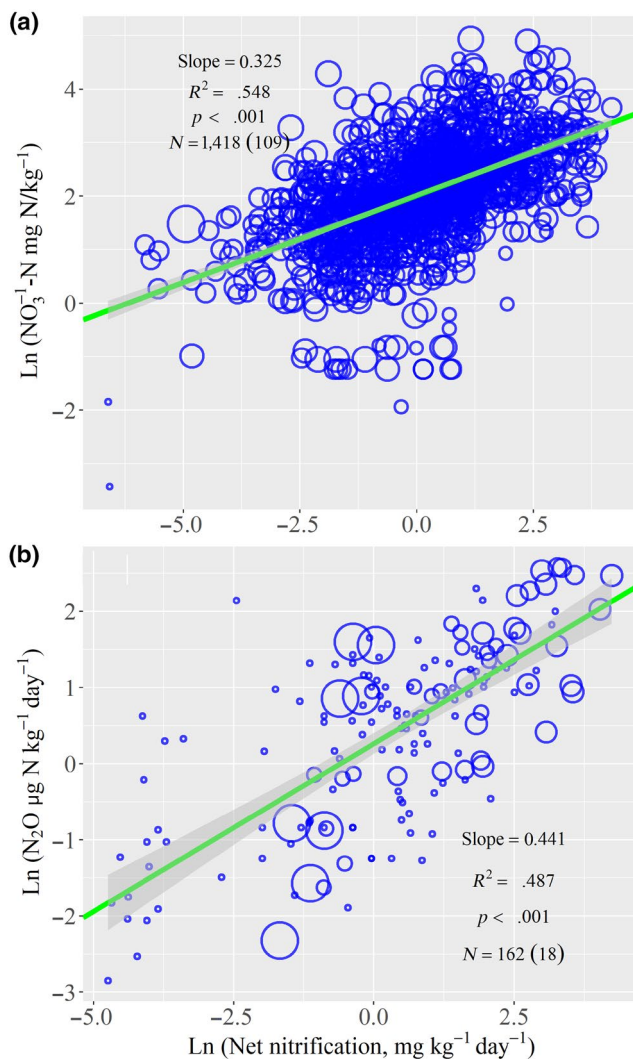


FIGURE 6 The bivariate relationships between the content of soil nitrate and soil nitrification rate (a), and the relationships between the emission of nitrous oxide and soil nitrification rate (b) at a global scale using logarithmically transformed data. The green lines are the slopes from the linear mixed effects models and the gray shadings are the 95% confidence intervals. The size of circles is the number of replicates from 1 to 30 (a) and from 3 to 15 (b). The number without parentheses is the amount of observations and the number with parentheses is the amount of studies [Colour figure can be viewed at wileyonlinelibrary.com]

study documents that nitrogen mineralization is the most important driver of soil nitrification rate (Hu et al., 2016). However, in the structural equation models in this study, the content of soil ammonium did not significantly relate to soil nitrification rate (standardized coefficient = 0.024, $p = .184$, data not shown). Moreover, the bivariate relationship between soil nitrification rate and soil ammonium was significantly positive in natural ecosystems in this study (Figure S3a), but the relationship was insignificant in croplands (Figure S3b). It may be caused by the giant inputs of inorganic nitrogen from fertilization that exceeds the capacity of soil nitrification in croplands. Although the addition of soil ammonium could stimulate soil nitrification rate in croplands with low TN (Figure 1b), the surplus soil ammonium may go through other nitrogen processes rather than soil nitrification. For instance, the emission of ammonia caused by anthropogenic management accounts for more than 60% of total emission (Vitousek et al., 1997). It supports the first hypothesis that the role of TN is greater than that of soil ammonium in global soil nitrification rate.

Soil MBN is one of the primary determinants of soil nitrification rate at a global scale, which is consistent with the findings in nine forest soils along a 3,700 km transect in Eastern China using the ^{15}N -labeling approach (Wang, Wang, et al., 2018). The positive relationship between soil nitrification rate and MBN is also confirmed in forest soils along an elevation in the Cordillera de Consuelo (Baldos, Corre, & Veldkamp, 2015). The potential mechanism is that higher soil microbial biomass stimulates soil nitrification by accelerating soil nitrogen mineralization. Across terrestrial ecosystems, there is a significantly positive relationship between soil nitrification and nitrogen mineralization (Booth, Stark, & Rastetter, 2005), and high soil microbial biomass stimulates soil nitrogen mineralization (Li et al., 2019). Moreover, MAP, TN and soil pH indirectly influence soil nitrification rate by changing soil MBN (Figure 5), which confirms the second hypothesis.

Mean annual temperature is the second important driver of global soil nitrification rate. A meta-analysis reveals that warming significantly increases net soil nitrification rate by 32.2% at the global scale (Bai et al., 2013) and by 56% on the Tibetan Plateau (Zhang, Shen, & Fu, 2015). Warming has positive effects on ammonia-oxidizing archaea community (Hu et al., 2016), which leads to a greater soil nitrification rate (Nguyen et al., 2019). Moreover, increase of net nitrogen mineralization under warming (52.2%; Bai et al., 2013) would provide more substrates for soil nitrification, because a part of nitrogen mineralized from organic nitrogen can be immediately nitrified (e.g., 25% in New England forest; Butler et al., 2012).

Soil pH is another important driver of global soil nitrification rate. Previous studies have reported that soil pH significantly influences soil nitrification (Li, Chapman, Nicol, & Yao, 2018; Wang, Zhang, et al., 2018). For instance, Wang et al. (2019) revealed that significantly higher soil nitrification occurs in alkaline soil ($7.04 \text{ mg N kg}^{-1} \text{ day}^{-1}$, $\text{pH} = 8.0$) than that in neutral ($2.31 \text{ mg N kg}^{-1} \text{ day}^{-1}$, $\text{pH} = 7.3$) and acidic soil ($-0.23 \text{ mg N kg}^{-1} \text{ day}^{-1}$, $\text{pH} = 5.7$). This may be due to two potential reasons. First, the lower soil pH dampens the soil microbial activity of nitrification. The richness and diversity of autotrophic oxidizing bacteria and archaea decrease with soil pH ranging from

8.5 to 4 (Hu, Zhang, Dai, Di, & He, 2013). The increasing soil pH could significantly increase ammonia-oxidizing abundance and potential nitrification (Zhang et al., 2017). Second, the content of TN negatively correlates with soil pH at spatial scales (Wang, Wang, & Ouyang, 2012), thereby, soil with lower pH may provide less substrate for soil nitrification.

4.2 | Implications for soil nitrification and nitrous oxide emission

Changes in TN and MBN will ultimately influence soil nitrification under anthropogenic disturbances. Higher autotrophic nitrification is observed in no-tillage soil compared with conventional tillage, which is due to the increase of TN (Liu et al., 2017). The compaction of forest soil reduces soil MBN by 8%–32%, and thus reduces net nitrification by 23%–60% (Tan, Chang, & Kabzems, 2005). Disturbances reduce soil microbial biomass by an average of 29.4%, with 48.7% following fires, 19.1% after harvest, and 41.7% under storms (Holden & Treseder, 2013), which may consequently decrease soil nitrification.

Global warming may increase soil nitrification rate. Our findings revealed that nitrification rate increased with temperature (Figures 2 and 5), which resulted in increased soil nitrate content. Increasing soil nitrogen availability leads to profound consequences for ecosystems. First, plant growth in terrestrial ecosystems is usually nitrogen limited (Reich, Hobbie, & Lee, 2014). The increase of soil available nitrogen will increase net primary production (Norby, Warren, Iversen, Medlyn, & McMurtrie, 2010). Second, increasing soil nitrogen availability will alter the plant community by changing plant competition and species composition (Farrer & Suding, 2016; Yang et al., 2011). In the long run, nitrophilic species (e.g., grasses) will benefit from the increasing soil nitrogen availability, whereas less nitrophilic species (e.g., forbs of small stature) will be suppressed (Bobbink et al., 2010).

The increasingly serious soil acidification may dampen soil nitrification rate. Nitrogen deposition decreases soil pH in terrestrial ecosystems (Stevens et al., 2011). The worldwide deposition of nitrogen is likely to significantly increase in the future (Reay, Dentener, Smith, Grace, & Feely, 2008), which will strengthen soil acidification. The soil microbial biomass is sharply depressed by soil acidification at soil $\text{pH} \leq 5$ (Meng et al., 2019; Pietri & Brookes, 2008), and the transcript copies of ammonia-oxidizing bacteria decrease with soil pH decreasing from 6.9 to 4.9 (Nicol, Leininger, Schleper, & Prosser, 2008). Therefore, soil acidification remarkably impedes soil nitrification (Cheng et al., 2013). Soil nitrification in croplands may be weakened more severely than that of natural ecosystems. As reported, soil pH decreases by 0.5 in croplands (Guo et al., 2010) and 0.26 in natural ecosystems (Tian & Niu, 2015). Thereby, soil acidification of croplands will dampen soil nitrification rate more severely.

Jointly considering climatic factors, soil properties, and microbial biomass characteristics will improve the prediction of soil

nitrification. Studies that only consider a few variables may elicit divergent results. To date, most nitrogen cycling models only consider temperature, water, and soil ammonium contents to calculate soil nitrification (Tian et al., 2018). Our structural equation model showed that TN and MBN are both important to affect soil nitrification rate (Figure 5). Therefore, the next generation model to simulate soil nitrification should comprehensively consider climate, soil properties, and microbial characteristics and their interactions.

Understanding global soil nitrification can facilitate the projection of soil nitrous oxide emissions as well. Previous studies on the prediction of soil nitrous oxide emissions used soil physical and chemical properties as predictors (Bouwman, Boumans, & Batjes, 2002), while few considered ecosystem processes, e.g., nitrification and denitrification. The SEMs of soil nitrification considering climate, soil properties, and microbial biomass in this study would benefit the projection of soil nitrous oxide emission.

4.3 | Uncertainties

We are aware that there may be some uncertainties in this study. First, while soil nitrification is performed by nitrifiers (Kuypers et al., 2018), ammonia-oxidizing microorganisms may be the most important as ammonium oxidation is the rate-limiting step in nitrification (Shen, Zhang, Di, & He, 2012). However, the diversity and abundance of soil ammonia-oxidizing microorganisms were not included in this synthesis due to data paucity. Second, our dataset includes only 80 observations from wetlands, which is much less compared with croplands (1,423), forests (841), and grasslands (368). The projections of soil nitrification in wetlands using our findings should be cautious. Third, net soil nitrification was measured in laboratory under optima conditions, e.g., 60% of water holding capacity (2,519 out of 3,140 observations), therefore, the global mean rate of soil nitrification might be overestimated when compared with those in the field condition.

This study provides a comprehensive evaluation of global potential soil nitrification rate and its drivers. In contrast to the finding that soil ammonium is the main substrate and controller of soil nitrification in previous models (Tian et al., 2018), we found that the content of soil total nitrogen is the predominant driver for the global variation of soil nitrification rate. MBN is of nearly equivalent importance relative to climatic factors and soil pH in predicting soil nitrification rate at a global scale, whereby climatic factors and soil properties influence soil nitrification/nitrate by changing soil MBN. The models integrating climatic factors, soil properties, and microbial biomass characteristics will enhance the accuracy of projection of soil nitrification rate under global change, which will promote accurate estimation of global nitrous oxide emission.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

Data supporting the results can be found in the Supporting Information.

ORCID

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

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

Yiqi Luo  <https://orcid.org/0000-0002-4556-0218>

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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