






## PRIMARY RESEARCH ARTICLE

# Vital roles of soil microbes in driving terrestrial nitrogen immobilization

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## Abstract

Nitrogen immobilization usually leads to nitrogen retention in soil and, thus, influences soil nitrogen supply for plant growth. Understanding soil nitrogen immobilization is important for predicting soil nitrogen cycling under anthropogenic activities and climate changes. However, the global patterns and drivers of soil nitrogen immobilization remain unclear. We synthesized 1350 observations of gross soil nitrogen immobilization rate (NIR) from 97 articles to identify patterns and drivers of NIR. The global mean NIR was  $8.77 \pm 1.01$  mg N kg<sup>-1</sup> soil day<sup>-1</sup>. It was  $5.55 \pm 0.41$  mg N kg<sup>-1</sup> soil day<sup>-1</sup> in croplands,  $15.74 \pm 3.02$  mg N kg<sup>-1</sup> soil day<sup>-1</sup> in wetlands, and  $15.26 \pm 2.98$  mg N kg<sup>-1</sup> soil day<sup>-1</sup> in forests. The NIR increased with mean annual temperature, precipitation, soil moisture, soil organic carbon, total nitrogen, dissolved organic nitrogen, ammonium, nitrate, phosphorus, and microbial biomass carbon. But it decreased with soil pH. The results of structural equation models showed that soil microbial biomass carbon was a pivotal driver of NIR, because temperature, total soil nitrogen, and soil pH mostly indirectly influenced NIR via changing soil microbial biomass. Moreover, microbial biomass carbon accounted for most of the variations in NIR among all direct relationships. Furthermore, the efficiency of transforming the immobilized nitrogen to microbial biomass nitrogen was lower in croplands than in natural ecosystems (i.e., forests, grasslands, and wetlands). These findings suggested that soil nitrogen retention may decrease under the land use change from forests or wetlands to croplands,

but NIR was expected to increase due to increased microbial biomass under global warming. The identified patterns and drivers of soil nitrogen immobilization in this study are crucial to project the changes in soil nitrogen retention.

#### KEYWORDS

croplands, global change, microbial biomass, nitrogen immobilization, soil nitrogen retention

## 1 | INTRODUCTION

Nitrogen availability is one of the important factors to regulate terrestrial primary production (Cleveland et al., 2013; Fernandez-Martinez et al., 2014). Recent studies have revealed that soil internal cycling processes supply more nitrogen for plant growth than fertilization within 1 year (Quan et al., 2020; Yan et al., 2020). It indicates that soil nitrogen retention capacity plays an essential role in supplying nitrogen to plants. As a key process of soil nitrogen retention, soil nitrogen immobilization refers to the transformation of inorganic nitrogen into the organic state (Jansson & Persson, 1982). The soil nitrogen immobilization retains nitrogen in soil to prevent leaching to water or emitting to atmosphere. Gross immobilization is more than 1400 Tg N year<sup>-1</sup> in terrestrial ecosystems (Kuypers et al., 2018). The immobilized nitrogen can be remineralized to provide nitrogen for plant growth (Quan et al., 2020). A recent study speculated that soil nitrogen immobilization might be hampered under global warming based on changes of other soil nitrogen processes while gross soil nitrogen immobilization rate (NIR) was not directly tested (Dai et al., 2020). It is urgent to directly examine gross soil NIR and identify its patterns and drivers at the global scale.

Soil nitrogen immobilization may be influenced by climate, soil physical and chemical properties. For example, it has been shown that NIR increases as temperature increases from 10°C to 15°C in most soils (Lang et al., 2010). NIR also increases by several fold when soil moisture increases from 30% to 60% (Sun et al., 2019). Among soil properties, soil pH is reported to account for 38%–41% of the variance in NIR (Wang et al., 2019). The quantity and quality of soil organic matter also affect soil NIR, such as nitrate immobilization enhanced under organic carbon addition at rates >500 mg C kg<sup>-1</sup> (Cheng et al., 2017). The NIR increases under organic matter addition with carbon:nitrogen ratios >18 (Cheng et al., 2017). The added substrates, for example, nitrate and ammonium, also promote NIR in tundra and boreal forests (Lavoie et al., 2011). Results from local studies are yet to be synthesized to reveal drivers of soil NIR at regional and global scales.

Soil microorganisms play an important role in nitrogen immobilization as the biotic immobilization by microbes largely contributed to total soil nitrogen immobilization (Johnson et al., 2000). In comparison, abiotic immobilization is usually in the range of 0.09–0.80 mg N kg<sup>-1</sup> soil in a 12-h incubation and only contributed less than 20% to the total immobilization (Barrett et al., 2002). A previous study found that heterotrophic microbes, an important type of soil microbes, participate in soil nitrogen immobilization (Burger & Jackson, 2003). Moreover, a study using an isotopic tracer technique

found both soil bacteria and fungi can immobilize soil inorganic nitrogen from the surrounding environments (Li, Li, et al., 2020). As so many microbes participate in soil nitrogen immobilization, therefore, soil microbial biomass is assumed to chiefly determine soil nitrogen immobilization. A significantly positive relationship between soil nitrate immobilization rate and fungal biomass was detected in forest soil (Zhu et al., 2013). Similarly, soil nitrogen immobilization increased with greater soil microbial biomass in an arable topsoil (Bargmann et al., 2014). All these studies suggest an important role of soil microorganisms in nitrogen immobilization, which is yet to be identified at the global scale.

In this study, we constructed a dataset through compiling the available data of NIR (1350 observations from 97 articles) in terrestrial ecosystems, including croplands, forests, grasslands, and wetlands. Three specific questions were addressed in this study: (1) What are the global patterns of NIR in terrestrial ecosystems? (2) How do climatic factors, soil physical and chemical properties, and microbial biomass affect NIR at a global scale? (3) Which factor is the main driver on terrestrial NIR?

## 2 | MATERIALS AND METHODS

### 2.1 | The construction of the NIR dataset

The dataset of NIR was constructed by compiling experimental data from published articles. Peer-reviewed articles were retrieved by means of two platforms: Web of Science and China National Knowledge Infrastructure Database. The keywords to search papers were 'Immobilization' AND 'Soil' AND 'Nitrogen'. To avoid the omission of published articles, we also used 'Ammonium immobilization' and 'Nitrate immobilization' as the terms to retrieve papers by means of Google Scholar. The duplications of papers were removed. Finally, 611 articles in English and 138 articles in Chinese remained. The retrieval of articles was completed by the end of May 2020. The criteria for eligible articles were: (1) Microbial NIRs were measured with the <sup>15</sup>N isotopic pool dilution approach. (2) Microbial NIRs were measured using the top layer soil (0–15 cm). (3) The NIR was available in the article or was calculated as the sum of ammonium immobilization rate and nitrate immobilization rate in the same experiment.

To examine the patterns and drivers of NIR, site-specific details were also collected. Climatic factors, for example, mean annual temperature and mean annual precipitation, either came from articles or were replenished from the climatic database (<http://www.worldclim.org>) based on geographical information. Soil properties included

soil texture, pH, soil organic carbon, total nitrogen, the ratio of soil carbon to nitrogen, dissolved organic carbon, dissolved organic nitrogen, available phosphorus, ammonium, and nitrate. Microbial characteristics included microbial biomass carbon, microbial biomass nitrogen, and the ratio of carbon to nitrogen of microbes. Soil properties and microbial characteristics were directly extracted from the original articles. We also collected the information of ecosystem types and experimental replications. All original data were extracted from the main text or appendix of peer-reviewed articles.

## 2.2 | Survey of data

There were 1350 observations of NIR from 97 articles after papers sifted. The observations were found to be distributed across all continents except Antarctica (Figure S1), mainly in Europe (329 observations), Asia (285 observations), and North America (257 observations). The number of observations from Africa, Australia, and South America was only 42, 58, and 7, respectively. Other observations lacked geographical details. The dataset encompassed four ecosystem types, namely croplands, forests, grasslands, and wetlands. To be specific, the number of observations from croplands, forests, grasslands, and wetlands was 420, 442, 402, and 71, respectively. Fifteen observations without the ecosystem information were categorized into the unclassified group. Climatic factors and basic soil properties varied largely. The mean annual temperature ranged from  $-5.4^{\circ}\text{C}$  to  $19.6^{\circ}\text{C}$ . The mean annual precipitation ranged from 140 to 7000 mm. The soil sand content varied from 0.7% to 94.5%. The range of soil pH was from 3.0 to 9.5. Soil moisture ranged from 30% to 100%.

## 2.3 | Statistical analyses

The incubation temperature varied in our dataset, in which the proportion of experiments under  $25^{\circ}\text{C}$  was nearly 50%. We normalized all rates of gross soil nitrogen immobilization to  $25^{\circ}\text{C}$  on the basis of the temperature sensitivity of soil nitrogen immobilization. The temperature sensitivity of NIR, 1.70, was an averaged value from previous studies (Cheng et al., 2015; Lang et al., 2010).

### 2.3.1 | Comparison of gross soil nitrogen immobilization among ecosystems

The observations of gross soil nitrogen immobilization were grouped into five ecosystem types, that is, croplands, forests, grasslands, wetlands, and unclassified ecosystem. Since the number of observations in the unclassified ecosystem (only accounting for 1.1% of total observations) was much less than those of classified ecosystems, we did not perform statistical analysis for the unclassified ecosystem. The averaged NIR of individual ecosystem was compared using one-way ANOVA and post hoc comparisons were performed using *TukeyHSD*. The statistically significant level was set at  $p < 0.05$ .

### 2.3.2 | Bivariate relationships of NIR against environmental factors

The bivariate relationships between NIR and environmental factors (climatic factors, soil properties, microbial biomass) were explored using linear mixed-effect models. The formula used in this study was:

$$\ln(\text{NIR}) = \beta_0 + \beta_1 \times \ln X + \pi_{\text{study}} + \varepsilon, \quad (1)$$

where NIR is the gross soil nitrogen immobilization rate,  $\ln X$  is the logarithm of each environmental factor,  $\beta_0$  is the intercept,  $\beta_1$  is the slope value,  $\pi_{\text{study}}$  is the random effect that can take into account the auto-correlation of observations in the same study, and  $\varepsilon$  is the sampling error. Due to the small number of microbial biomass carbon:microbial biomass nitrogen ratio, we did not analyze the relationship of NIR against carbon:nitrogen ratio of microbial biomass.

### 2.3.3 | Multiple relationships of NIR with environmental factors

We constructed the concept framework of structural equation models (SEMs) on the basis of the bivariate relationships between NIR and environmental factors. In the concept framework of SEMs, the rate of gross soil nitrogen immobilization was directly influenced by climatic factors (mean annual temperature, mean annual precipitation), soil physical and/or chemical properties (soil sand content, soil pH, soil moisture), soil carbon and nutrients (soil organic carbon, dissolved organic carbon, total nitrogen, dissolved organic nitrogen, ammonium, nitrate, the ratio of carbon to nitrogen, and soil available phosphorus), and soil microbial biomass (e.g., microbial biomass carbon). The environmental factors may firstly influence the soil microbial biomass and subsequently influence NIR. In order to compare the contribution of each variable to NIR, all data were normalized (Z-score normalization) in SEMs after data were logarithm-transformed. In SEMs, the fixed variables were the environmental factors, the random variable was the "Study," the weight was the replications of each observation. In the initial SEMs, all variables were taken into consideration, but the models were not eligible. Since the initial SEMs were replete with redundant variables, the SEMs were optimized by reducing variables step by step. Finally, we removed the redundant variables in the optimal SEMs. The optimal SEMs were evaluated by two indicators, Akaike information criterion value and  $p$  value. In this study, the Akaike information criterion value and  $p$  value of optimal SEMs were 41.7 and 0.46, respectively. All SEMs were tested by the *piecewiseSEM* package.

### 2.3.4 | Bivariate relationships of microbial biomass nitrogen with NIR

First, we analyzed the bivariate relationship between microbial biomass nitrogen and NIR at a global scale using all the data.

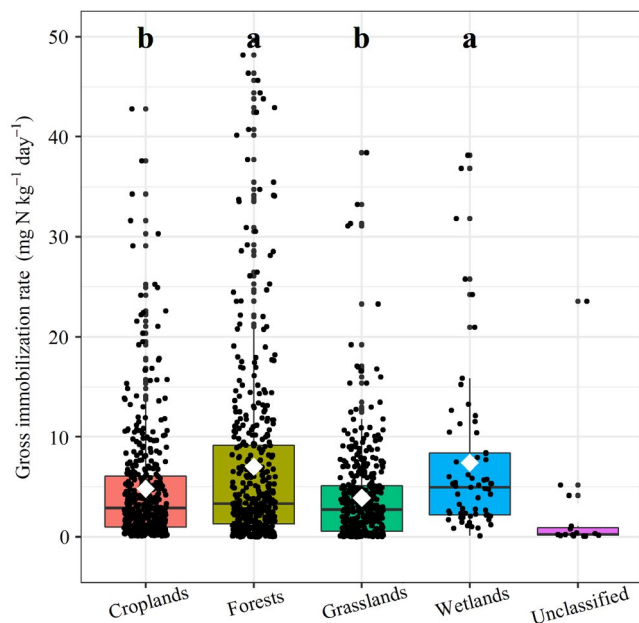
$$\ln(\text{microbial biomass nitrogen}) = \beta_0 + \beta_1 \times \ln X + \pi_{\text{study}} + \varepsilon, \quad (2)$$

where  $\ln X$  is the logarithm of NIR,  $\beta_0$  is the intercept,  $\beta_1$  is the slope value,  $\pi_{\text{study}}$  is the random effect that can take into account the autocorrelation of observations in the same study, and  $\varepsilon$  is the sampling error. Second, we grouped data into different ecosystem types and analyzed this relationship in each ecosystem. To visually compare the differences of the regression slope value in different ecosystems, we normalized the microbial biomass nitrogen and NIR in each individual ecosystem. In unclassified ecosystems, we did not conduct this analysis, because there were only 13 observations from two articles.

### 3 | RESULTS

#### 3.1 | Comparisons of NIR among ecosystems

The averaged NIR was  $8.77 \pm 1.01 \text{ mg N kg}^{-1} \text{ soil day}^{-1}$  at the global scale. In each ecosystem type, soil NIR varied largely (Figure 1). In general, the mean rates of gross soil nitrogen immobilization were the greatest in wetlands and forests, namely  $15.74 \pm 3.02$  and  $15.26 \pm 2.98 \text{ mg N kg}^{-1} \text{ soil day}^{-1}$ , respectively. There were no significant differences between NIR in these two ecosystems ( $p = 0.99$ ). The NIR in croplands,  $5.55 \pm 0.41 \text{ mg N kg}^{-1} \text{ soil day}^{-1}$ , was significantly lower than those of wetlands and forests ( $p < 0.001$ ). The NIR of grasslands ( $3.89 \pm 0.24 \text{ mg N kg}^{-1} \text{ soil day}^{-1}$ ) was significantly lower



**FIGURE 1** Comparisons of gross soil N immobilization rates among ecosystem types, that is, croplands, forests, grasslands, wetlands, and unclassified ecosystems. The black dot stands for the individual gross soil N immobilization rate, and the diamond stands for the average N immobilization rate in each ecosystem. Different lowercase letters above the boxplot indicate that gross soil N immobilization rate differs significantly between ecosystem types ( $p < 0.05$ ) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

than those of wetlands and forests ( $p < 0.001$ ), but did not differ significantly with that of croplands ( $p = 0.92$ ).

#### 3.2 | Bivariate relations between NIR and environmental variables

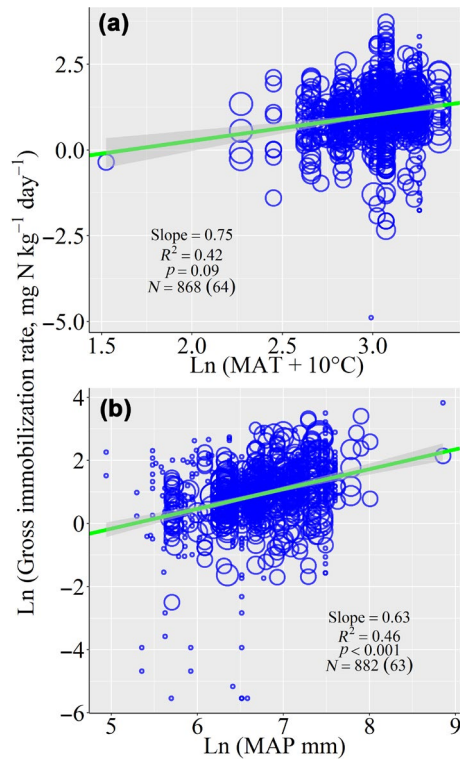
The rate of gross soil nitrogen immobilization tended to increase with higher mean annual temperature at the global scale (Figure 2), with the slope being marginally significant from zero (the number of observations [ $N$ ] = 868,  $p = 0.09$ ; Figure 2a), and the relationship between NIR and mean annual temperature was weaker when the observations with the lowest temperature were excluded ( $p = 0.22$ ). There were greater NIR with higher mean annual precipitation at a global scale ( $N = 882$ ,  $p < 0.001$ ; Figure 2b).

Generally, soil physical and chemical properties significantly associated with the NIR at a global scale (Figure 3). The NIR decreased with higher soil pH ( $N = 1084$ ,  $p = 0.02$ ; Figure 3b), yet NIR increased with higher soil moisture ( $N = 607$ ,  $p = 0.03$ ; Figure 3c). Soil texture did not significantly affect NIR. There was no significant relationship between NIR and soil sand content at the global scale ( $N = 419$ ,  $p = 0.79$ ; Figure 3a).

Soil organic carbon, nutrients, and microbial biomass also significantly influenced the rate of gross soil nitrogen immobilization at the global scale (Figure 4). The NIR accelerated with higher soil organic carbon content ( $N = 1064$ ,  $p < 0.001$ ; Figure 4a) and total soil nitrogen content ( $N = 1030$ ,  $p < 0.001$ ; Figure 4b). Soil NIR increased with higher soil carbon:nitrogen ratio ( $N = 999$ ,  $p = 0.02$ ; Figure 4c). The higher concentrations of dissolved soil organic carbon ( $N = 96$ ,  $p = 0.03$ ; Figure 4d) and nitrogen ( $N = 110$ ,  $p = 0.05$ ; Figure 4e) could increase the rate of gross soil nitrogen immobilization. More available soil phosphorus also accelerated NIR at the global scale ( $N = 95$ ,  $p = 0.02$ ; Figure 4f). The NIR could increase with higher concentrations of soil inorganic nitrogen, that is, ammonium ( $N = 857$ ,  $p = 0.02$ ; Figure 4g) and nitrate ( $N = 897$ ,  $p < 0.001$ ; Figure 4h). More importantly, NIR substantially increased with higher soil microbial biomass carbon at the global scale with the slope value being 0.89 ( $N = 247$ ,  $p < 0.001$ ; Figure 4i).

#### 3.3 | Multivariable relationships of NIR with environmental variables

Soil microbial biomass was the pivotal driver of NIR at the global scale (Figure 5). Among the direct relationships in SEMs, the influence of soil microbial biomass on NIR was the greatest (standard coefficient = 0.18,  $p < 0.001$ ), whereby higher soil microbial biomass carbon significantly accelerated NIR, which could account for 21.2% variance of global NIR. The second important driver was total soil nitrogen content, with the standard coefficient value being 0.17 ( $p < 0.001$ ). The substrates of microbial nitrogen immobilization, both soil ammonium and nitrate, could explain 15.3% variance of gross soil nitrogen immobilization (joint standard



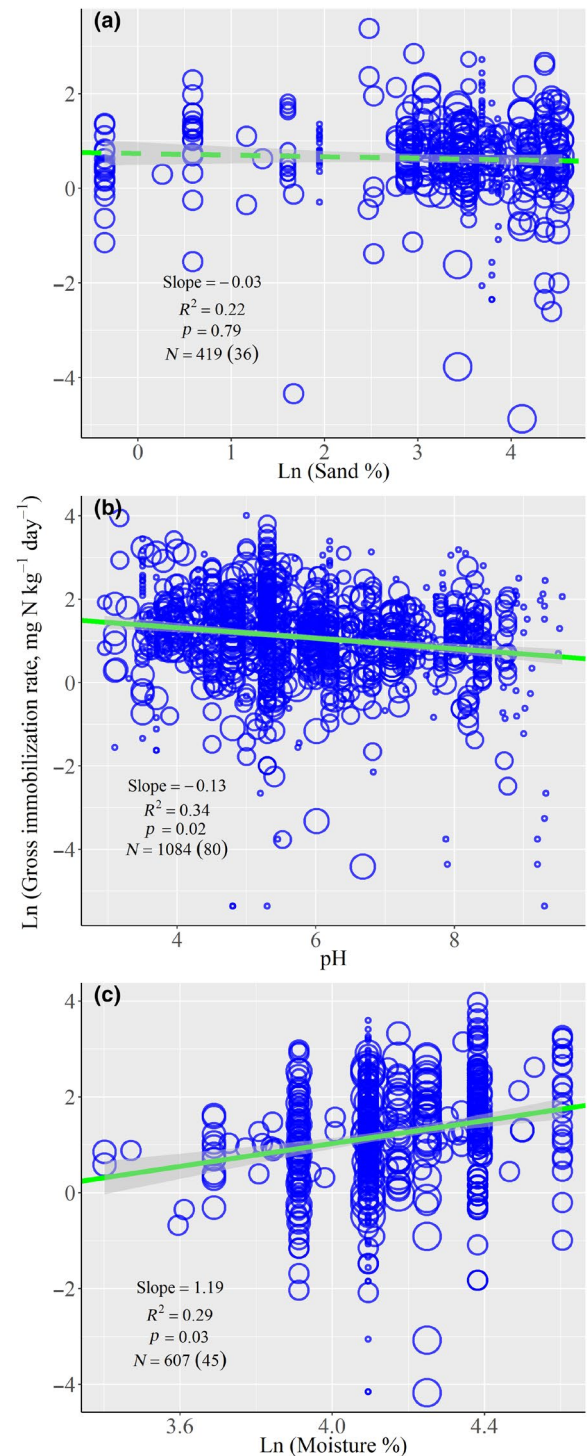
**FIGURE 2** Bivariate relations of gross soil N immobilization rate with mean annual temperature (MAT, a) and precipitation (MAP, b) at the global scale. Regressions were conducted on the basis of logarithmically transformed data. The solid line is the slope, and the gray shadow stands for 95% confidence intervals. The size of dots stands for the value of replicates ranging from 1 to 12. Values after *N* are the number of observations without parentheses and the number of studies with parentheses, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

coefficient = 0.13, both  $p < 0.05$ ). The better hydrothermal condition also expedited NIR, and the standard coefficients for mean annual temperature, mean annual precipitation, and soil moisture were 0.12 ( $p = 0.002$ ), 0.15 ( $p < 0.001$ ), and 0.10 ( $p = 0.002$ ), respectively.

Climatic factors and soil properties influenced NIR mainly via soil microbial biomass. Greater mean annual temperature, soil pH, and soil total nitrogen content likely increased soil microbial biomass carbon content and then positively affected NIR. In comparison to the direct effects on NIR (standard coefficient = 0.17,  $p < 0.001$ ), soil total nitrogen more likely influenced soil microbial biomass (standard coefficient = 0.36,  $p < 0.001$ ) and then indirectly affected NIR.

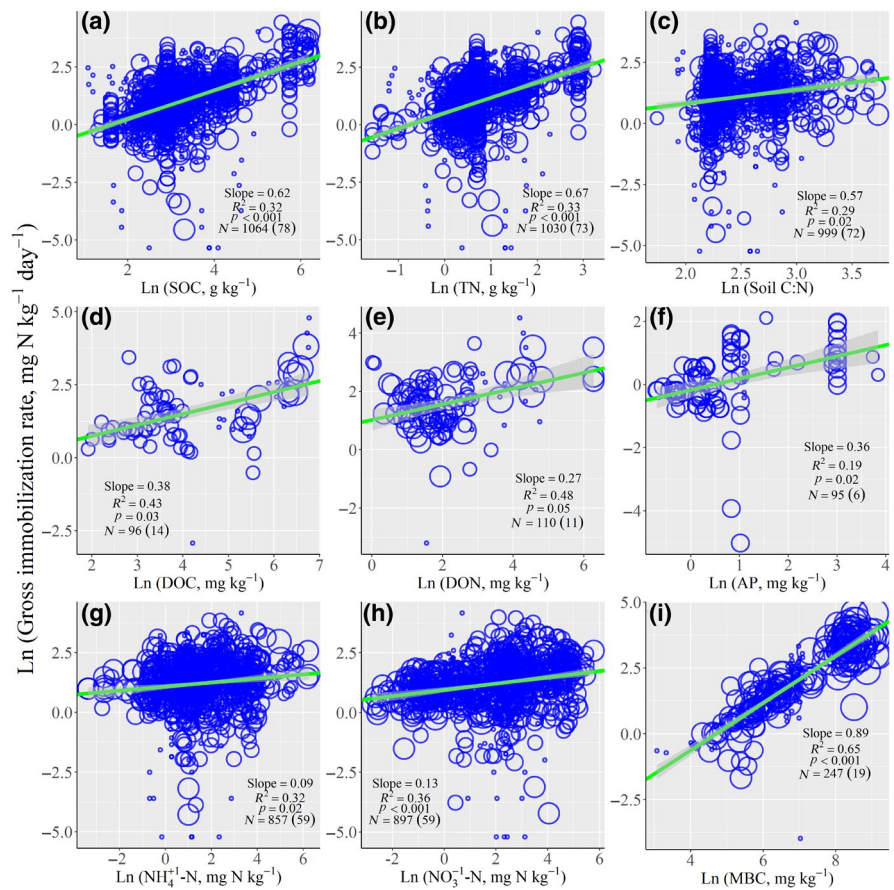
### 3.4 | Bivariate relationships between soil microbial biomass nitrogen and NIR across ecosystem types

There was a significantly positive relationship between soil microbial biomass nitrogen content and NIR across all studies ( $N = 288$ ,  $p < 0.001$ , Figure 6a) and in each ecosystem type (Figure 6b). The

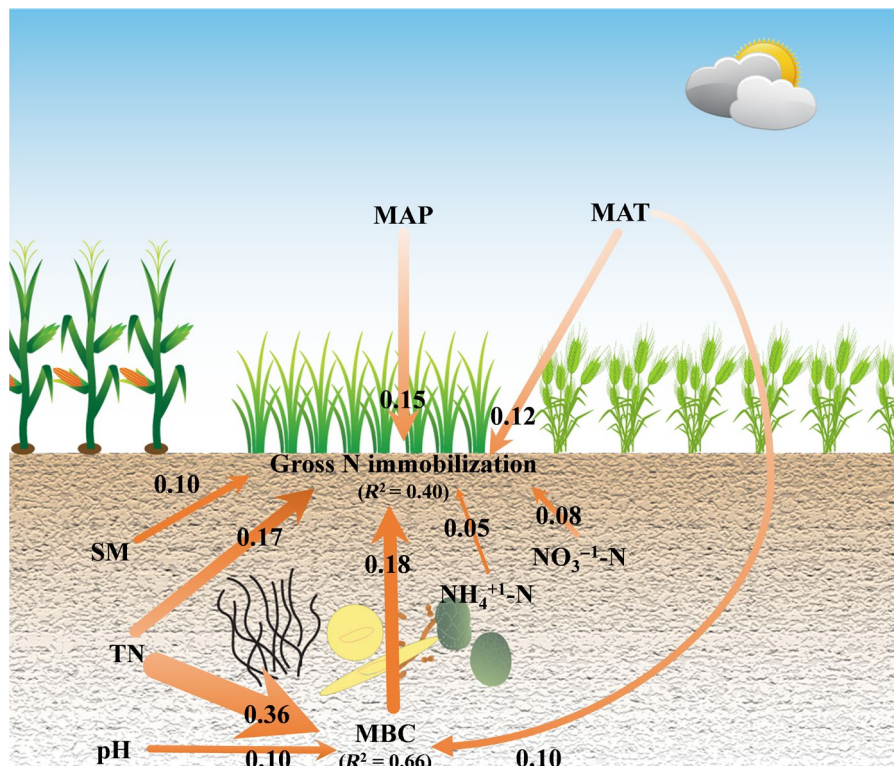


**FIGURE 3** Bivariate relations of gross soil N immobilization rate with soil properties at the global scale, that is, soil sand content (a), pH (b), and soil moisture (c). Regressions were conducted on the basis of logarithmically transformed data in (a) and (c). Solid lines are significant slopes, whereas the dashed line is the insignificant slope. The gray shadow stands for 95% confidence intervals. The size of dots stands for the value of replicates ranging from 1 to 12. Values after *N* are the number of observations without parentheses and the number of studies with parentheses, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**FIGURE 4** Bivariate relations of gross soil N immobilization rate with soil organic carbon (a), total soil nitrogen (b), the ratio of soil carbon to nitrogen (c), soil dissolved organic carbon (d), dissolved organic nitrogen (e), available phosphorus (f), ammonium contents (g), nitrate contents (h), and soil microbial biomass carbon (i). Regressions were conducted using logarithmically transformed data. Solid lines are the significant slopes. The gray shadow stands for 95% confidence intervals. The size of dots stands for the value of replicates ranging from 1 to 12. Values after N are the number of observations without parentheses and the number of studies with parentheses, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



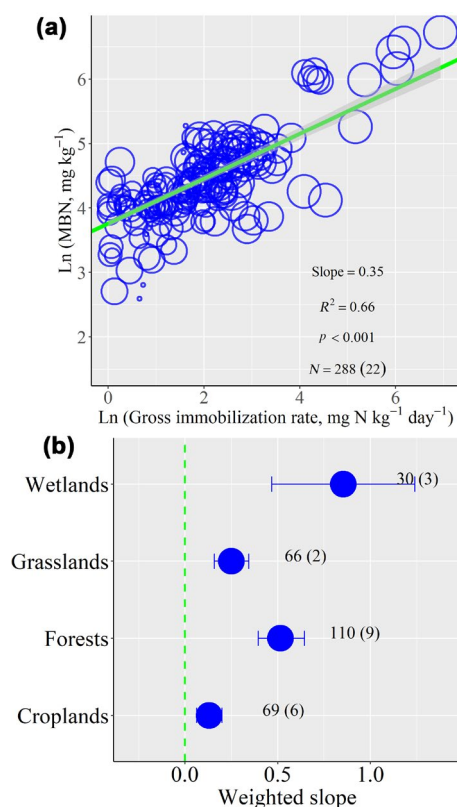
**FIGURE 5** Multiple relations of gross soil N immobilization rate with environmental factors at the global scale. Values are standardized coefficients from structural equation models. All relationships presented in this figure are statistically significant ( $p < 0.05$ ). The abbreviations of MAT, MAP, SM, TN, and MBC are mean annual temperature, mean annual precipitation, soil moisture, total soil nitrogen, and microbial biomass carbon, respectively. The Akaike information criterion value and  $p$ -value of SEMs were 41.7 and 0.46, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



weighted slope values for this relationship were  $0.13 \pm 0.07$  for croplands ( $N = 69$ ,  $p < 0.001$ ),  $0.51 \pm 0.13$  for forests ( $N = 110$ ,  $p < 0.001$ ),  $0.25 \pm 0.09$  for grasslands ( $N = 66$ ,  $p < 0.001$ ), and  $0.85 \pm 0.39$  for wetlands ( $N = 30$ ,  $p < 0.001$ ). Noteworthy, the weighted slope values were generally greater in natural ecosystems (i.e., forests, grasslands, and wetlands) than in croplands.

## 4 | DISCUSSION

This study is among the first attempts to explore the global patterns and drivers of NIR by compiling 1350 observations from terrestrial ecosystems. Soil microbial biomass carbon was identified as the pivotal driver in terrestrial NIR at the global scale. Soil NIR was found to increase due to increased soil microbial biomass carbon under global warming (Xu & Yuan, 2017) and increasing precipitation (Ren et al., 2017), but decreased under the land cover change from forests or wetlands to croplands. The identified drivers of soil nitrogen immobilization offer empirical evidence for improving soil nitrogen models to predict changes in soil nitrogen retention under global changes.



**FIGURE 6** Bivariate relation between soil microbial nitrogen contents and gross N immobilization rate in terrestrial ecosystems (a) and in individual ecosystem type (b). In (a), the size of dots stands for the value of replicates ranging from 1 to 12. In (b), the dot is the averaged slope and bars are 95% confidence intervals. Values after  $N$  are the number of observations without parentheses and the number of studies with parentheses, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

### 4.1 | Drivers of terrestrial gross soil nitrogen immobilization

Climatic factors, soil properties, and microbial biomass all significantly influence the NIR at the global scale. Among them, soil microbial biomass was found to play the most important role in influencing the gross soil nitrogen immobilization at the global scale (Figure 5). This is consistent with findings at the site level that microbial activity significantly drives NIR (Bengtsson et al., 2003). Microbes play a pivotal role in nitrogen immobilization likely due to the following reasons. First, nitrogen is the essential nutrient to soil microbes. In general, the nitrogen:carbon:phosphorus ratio of soil microbial biomass is 7:60:1 (Cleveland & Liptzin, 2007). Nitrogen may contribute approximately 10% of total elements in soil microbial biomass. Second, the ability of soil microbes to gain nitrogen is relatively high. As growth of microbial biomass requires nitrogen, soil microbes may preferentially acquire nitrogen from the environment. For example, at high altitude, soil microbes have a greater capacity to take up soil nitrogen than plants (Thebault et al., 2014). In arctic regions, 40%–49% of the labeled nitrogen is recovered in soil microbial biomass whereas <1% is recovered by plants (Nordin et al., 2004). Third, soil microbes play an important role in soil nitrogen mineralization (Li, Tian, et al., 2019) and nitrification (Li, Zeng, Tian, Wang, Fu, Wang, et al., 2020), by which microbes may more easily obtain the ammonium and nitrate from the environment.

Total soil nitrogen content was also found to influence NIR both directly and indirectly. In the direct pathway, total soil nitrogen provides substrates for microbial nitrogen immobilization, such as ammonium and nitrate. Soil organic nitrogen can be mineralized to ammonium or nitrified to nitrate, which consequently provides the substrates to microbial immobilization. At the global scale, soil organic nitrogen mainly drives soil nitrification rate (Li, Zeng, Tian, Wang, Fu, Zhang, et al., 2020), whereby the end product of nitrification may be taken up by microbes. In certain cases, soil microbes could assimilate some organic nitrogen from total soil nitrogen. For instance, soil microbes can take up glycine from soil (Liu et al., 2016). Total soil nitrogen content indirectly influences NIR as more soil nitrogen can harbor more soil microbes (Figure 5; Li, Tian, et al., 2019; Tahovska et al., 2020). More soil microbes promote soil nitrogen immobilization. We also found that the indirect influence was more important than the direct influence (Figure 5).

Substrates of soil nitrogen immobilization, for example, ammonium and nitrate, also impact NIR at the global scale. The joint effect of ammonium and nitrate on NIR was 0.13 (standard coefficient from SEMs), contributing 15.3% of the total direct effects. As the substrates of immobilization, higher concentrations of inorganic nitrogen can promote NIR. However, very high concentrations of soil ammonium or nitrate may hamper soil microbes, particularly under fertilization in croplands. For example, microbial biomass decreased by 5.8% under nitrogen addition reported by a global synthesis (Lu et al., 2011), and the more amount of fertilization could result in greater reduction of microbial biomass (Jia et al., 2020). Additionally, high nitrogen addition also reduces microbial diversity (Wang et al.,

2018). In our study, the higher soil ammonium and nitrate tended to show negative impacts on soil microbial biomass ( $-0.007$  and  $-0.003$ , respectively), due to 31% observations from croplands, although the effect did not reach the statistically significant level. Therefore, the negative effect of ammonium and/or nitrate on microbial biomass can partially counteract the positive effect of substrates on gross soil nitrogen immobilization.

Climatic factors also influence terrestrial gross soil nitrogen immobilization. High temperature and soil moisture accelerate soil NIR. In general, soil microbial metabolic activity increases with growing temperature (Li, Zeng, Tian, Wang, Fu, Wang, et al., 2020; Xu et al., 2017), and high soil moisture can promote soil bacterial growth (Nicola & Baath, 2019). In good hydrothermal environments where nitrogen mineralization and nitrification rate increase (Li, Tian, et al., 2019; Li, Zeng, Tian, Wang, Fu, Zhang, et al., 2020), more substrates are available for nitrogen immobilization. In addition, high temperature increased soil microbial biomass carbon (Figure 5), consistent with the results of a global meta-analysis that warming increases microbial biomass carbon by 3.6% (Xu & Yuan, 2017), which may promote soil nitrogen immobilization.

## 4.2 | Fate of soil immobilized nitrogen

Immobilized nitrogen (through soil nitrogen immobilization) may augment soil microbial biomass nitrogen. Positive relationships were found between soil microbial biomass nitrogen and NIR at the global scale and for each ecosystem type in this study (Figure 6). It indicated that the microbial biomass nitrogen was one important fate of immobilized nitrogen. Although soil microbial biomass nitrogen somehow concomitantly changes with microbial biomass carbon under environmental changes (e.g., Zhou et al., 2017), the carbon:nitrogen ratio of soil microbial biomass varied much from 2.39 to 16.00 in our data. Other studies also document that immobilized nitrogen can transform to microbial biomass nitrogen. For instance, fertilization with nitrogen increases the content of microbial biomass nitrogen (Gallardo & Schlesinger, 1995) and a great portion of labeled nitrogen is immobilized and transformed into microbial biomass as revealed by an isotopic study (Ma et al., 2016). An experiment shows that up to 138 mg nitrogen can be transformed into microbial biomass nitrogen under 200 mg N addition in a 3-day incubation (Vega-Jarquín et al., 2003). Thus, the majority of immobilized nitrogen may be transformed to microbial biomass nitrogen.

The immobilized nitrogen in microbial biomass can be remineralized or transformed to stable soil organic matter. Soil microbial biomass nitrogen is the transient pool for immobilized nitrogen in the short term. The microbial biomass turns over rapidly with the turnover time generally less than 1 year (Spohn et al., 2016). A recent study shows that the residence time of microbial biomass varies from 156 to 325 days (Chen et al., 2020). Therefore, immobilized nitrogen cannot always exist in the microbial biomass. A previous study found that the amounts of immobilized nitrogen are 64–92 mg N g<sup>-1</sup> C in different soil types, and the amounts of remineralized nitrogen are

0–50 mg N g<sup>-1</sup> C at the end of the experiment (300 days), with approximately 30% of immobilized nitrogen remaining in the microbial biomass (Vinten et al., 2002). Thus, a part of immobilized nitrogen can be remineralized to inorganic nitrogen (Paul & Juma, 1981). However, in the long run, some immobilized nitrogen can be transformed to stable soil organic matter. A recent study found that the fast turnover of microbial biomass can facilitate the accumulation of stable soil organic matter (Prommer et al., 2020). Using the isotopic approach, Wang et al. (2020) reveal that a portion of microbial necromass <sup>15</sup>N (both bacterial necromass and fungal necromass) is recovered in the mineral-associated organic matter fraction.

Immobilized nitrogen is transformed into microbial biomass with different efficiencies among ecosystems. The weighted slope of the relationship between soil microbial biomass nitrogen and NIR in croplands was lower than that in natural ecosystems (Figure 6). It suggests that a smaller portion of immobilized nitrogen is transformed into microbial biomass nitrogen in croplands possibly due to quick remineralization. The assimilation of inorganic nitrogen into microbial biomass is influenced by the soil carbon:nitrogen ratio, and the higher assimilation rate occurs in soil with a higher carbon:nitrogen ratio (Li, He, et al., 2019). In croplands, the fertilization of inorganic nitrogen reduces the soil carbon:nitrogen ratio (Deng et al., 2020). High nitrogen content in microbial biomass may result in low transformation efficiency of immobilized nitrogen into microbial biomass nitrogen in croplands. A global synthesis concluded that the carbon:nitrogen ratio of microbial biomass in croplands (7.2) is lower than the average value of natural ecosystems (e.g., 8.3 for boreal forest, 9.4 for tundra; Xu et al., 2013).

## 4.3 | Implications for soil nitrogen retention and uncertainties

Soil NIR can reflect the capacity of soil nitrogen retention. The land use change from forests or wetlands to croplands might decrease soil nitrogen retention capacity (Figure 1). The ratio of gross nitrification to ammonium immobilization rates and the ratios of gross nitrogen mineralization to immobilization rates in croplands are higher than those in the forests (Lang et al., 2019), indicating that nitrogen immobilization capacity lowers in soil nitrogen cycling in croplands. A recent study found that both fungal nitrate immobilization rate and bacterial immobilization rate significantly decrease by 81% and 61%, respectively, when forest is converted into cropland (Li, He, et al., 2019). Moreover, the transformation efficiency of immobilized nitrogen to microbial biomass nitrogen was also lower in croplands (Figure 6). The soil available nitrogen concentrations after a period under similar nitrogen inputs can also reflect soil nitrogen retention. A previous study found that the conversion of croplands to forests, shrublands, and grasslands increases soil nitrogen supply by 47%, 36%, and 24%, respectively (Tian et al., 2018). The above findings suggest that soils have a lower capacity to retain nitrogen in croplands.

Global warming may increase soil nitrogen immobilization via boosting microbial biomass carbon. In general, experimental



warming can significantly increase soil microbial biomass carbon by 2.2%–7.6% from a global synthesis (Lu et al., 2013). It may potentially increase NIR based on the positive relationship between NIR and microbial biomass carbon (Figure 4i). Nitrogen deposition may reduce soil microbial biomass and subsequently decrease soil nitrogen immobilization. As reported, soil microbial biomass decreases by 13.2% under nitrogen addition (Zhang et al., 2018). Soil microbial biomass is the immediate sink for inorganic nitrogen compared with root biomass and soil organic matter (Zogg et al., 2000). Therefore, nitrogen immobilization may decrease under nitrogen deposition, especially in the top soil (Cheng et al., 2020). Changes in microbial immobilization under nitrogen enrichment also vary with nitrogen addition levels (Song et al., 2021).

The results of this study have some uncertainties. First, there is a technical bottleneck to eliminate plant uptake in field measurements from gross nitrogen immobilization. As a result, data from field measurement are very rare in published studies. The NIR was measured in laboratory with the optimal incubation condition, which might overestimate the rate of gross soil nitrogen immobilization. Second, gross soil nitrogen immobilization includes ammonium immobilization and nitrate immobilization. But we did not separately explore their patterns and drivers due to data paucity. Third, the characteristics of soil microbial biomass, such as the ratio of microbial biomass carbon to microbial biomass nitrogen, may influence gross soil nitrogen immobilization. However, we are unable to explore the effect of microbial biomass carbon:nitrogen ratio in gross soil nitrogen immobilization at the global scale due to the data scarcity in this study.

Our study revealed that soil microbial biomass was the most important driver of NIR at the global scale. Temperature, total soil nitrogen, and soil pH influenced NIR via changing soil microbial biomass. The greater NIR could augment soil microbial biomass nitrogen across ecosystems. Soil nitrogen retention may reduce under the land use change from forests or wetlands to croplands because NIR was significantly lower and the transformation efficiency from immobilized nitrogen to microbial biomass nitrogen was also lower in croplands than in other ecosystems. We anticipate that gross soil nitrogen immobilization will likely increase due to increased soil microbial biomass under global warming. The identified key drivers and relationships in our study offer direct experimental evidence, which may be useful to improve nitrogen cycling models to better project the changes in soil nitrogen retention under global change.

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#### CONFLICT OF INTEREST

The authors declare no competing financial interests.

#### AUTHOR CONTRIBUTIONS

Zhaolei Li carried out the analyses. Zhaoli Li and Shuli Niu wrote the first draft of manuscript. All authors were greatly involved in writing.

#### DATA AVAILABILITY STATEMENT

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

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## SUPPORTING INFORMATION

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

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