

Soil nitrogen substrates determine global N₂O emission more than climate and other soil properties

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Abstract

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Abstract

Accurate estimation of N₂O emission is one of the primary objectives to project the warming potential. However, the global patterns and main controlling factors of soil N₂O emission remain elusive. We compiled a dataset with 6016 field observations from 219 articles and found that the averaged soil N₂O emission rate was $1111.8 \pm 26.59 \mu\text{g N m}^{-2} \text{ day}^{-1}$. Soil N₂O emission rates were significantly influenced by climatic factors (i.e. mean annual temperature), soil physical and chemical properties (e.g. pH, nitrate, ammonium, and total nitrogen), and microbial traits (microbial biomass nitrogen) at a global scale. The combined direct effects of soil nitrate, ammonium, and total nitrogen (combined standard coefficient = 0.45) accounted for the most variance of global soil N₂O emissions (total standard coefficient = 0.84). This study highlights the critical roles of soil nitrogen substrates on N₂O emission, which will be helpful to optimize the process-models on soil N₂O emissions.

Keywords:

Nitrous oxide emission; nitrate; ammonium; organic nitrogen; microbial biomass; warming

Introduction

Nitrous oxide (N₂O) is the third most important greenhouse gas, following carbon dioxide and methane. N₂O is a long-lived gas in atmosphere with an average lifetime of 116 ± 9 years (Prather *et al.* 2015), and the radiative forcing of N₂O per unit is up to 298 times larger than that of carbon dioxide on a 100-year timescale. Soil N₂O emission dominates the total N₂O emission at the global scale (Syakila & Kroeze 2011). Global soil N₂O emission increases by approximately 59% from preindustrial period to the recent decade (Tian *et al.* 2019) and will increase to 16 Tg N yr⁻¹ by 2050 (Bouwman *et al.* 2013). The N₂O forcing will increase by 1.7% when atmospheric N₂O concentrations reach 525 ppb (Etminan *et al.* 2016). To project the warming

potential, we need to accurately simulate soil N₂O emission. However, there are large uncertainties in the projections of soil N₂O emission (Del Grosso *et al.* 2010; Tian *et al.* 2019), which ranges from 3.3 to 13.3 Tg N yr⁻¹ using different models and the relative predictive error is up to 235% (Zhang *et al.* 2018). Moreover, the simulated N₂O emission does not match the observed data well (Zhang *et al.* 2018). To optimize the models, it is urgent to understand the drivers of soil N₂O emission at a global scale.

Soil N₂O comes from soil nitrification and denitrification, which can be regulated by climatic factors, soil physical and/or chemical properties, and microbial traits. Of climatic factors, higher temperature usually motivates soil N₂O emission in terrestrial ecosystems through denitrification (Zhang *et al.* 2019c; Wang *et al.* 2020). Mean annual temperature also significantly influences soil nitrification on the global scale (Li *et al.* 2020), which may eventually impact global soil N₂O emission. Since water condition affect both nitrification and denitrification *via* altering soil oxygen availability (Bollmann & Conrad 1998), higher soil water content significantly increases soil N₂O emission (Wu *et al.* 2017).

Comparing with climatic factors, the roles of soil properties on soil N₂O emission remain more controversial. Some studies found soil N₂O emission peaks at pH 6.5 and then decreases with increasing pH (Stevens *et al.* 1998), whereas another study showed that N₂O production remains constant with changing soil pH (Cuhel *et al.* 2010). The conflicting results are also reported about the effects of soil texture on N₂O emission. Although soil texture can impact soil N₂O emission in theory (Henault *et al.* 2012), N₂O emission does not change much with difference clay or sandy loam content in croplands (Syvasalo *et al.* 2004). Additionally, a recent study discovered soil cation exchange capacity regulates soil N₂O emission in croplands (Liu *et al.* 2019), but Kravchenko *et al.* (2002) pointed out that soil cation exchange capacity does not account for the fluctuations of soil N₂O emission.

As for soil microbes, at the local scale, soil N₂O emission may positively correlate with microbial biomass nitrogen (MBN) (Zhang *et al.* 2019a), but there is no obvious role of soil microbes on N₂O emission in arid regions (Yin *et al.* 2019). Therefore, it remains unclear how those climate and soil chemical and physical factors individually and interactively regulate soil N₂O emission, which requires a synthesis to reveal the mechanisms underlying the variations of global soil N₂O emission.

Even some ecosystem models tried to incorporate the role of climatic factors (*e.g.* precipitation) and soil properties (*e.g.* soil pH, bulk density, soil texture) (Werner *et al.* 2007), the simulated soil N₂O still fails to match the observed N₂O emission well (Dangalet *et al.* 2019). For instance, Fuchset *al.* (2020) points out the IPCC usually underestimates N₂O emission in an intensively managed grassland. The most of models may miss some important regulators, beside climate and soil properties, in driving soil N₂O emission. Theoretically, soil N content should be critical for N₂O emission since it provides substrate for producing N₂O. A recent global assessment using ensemble of terrestrial biosphere models also found that global N fertilizer application contributes 2.0 ± 0.8 Tg N₂O-N yr⁻¹ during 2007-2016, manure application contributes 0.6 ± 0.4 Tg N₂O-N yr⁻¹, and N deposition contributes 26% of global soil N₂O emission (Tian *et al.* 2019). Furthermore, the decreases in cropland-N₂O emissions after 2003 are mainly ascribed to the reduction in usage of N fertilizer in China (Shang *et al.* 2019). Therefore, we hypothesized that soil N contents might play an important role on regulating soil N₂O emissions at the global scale. In fact, some models have recognized the important roles of N substrates for soil N₂O emission, but used the amounts of fertilization (*e.g.* N fertilizer, manure, and N deposition) as input data (Tian *et al.* 2018) because the data of soil N contents are scarce and the relationships between soil N₂O emission and soil N contents are unclear. There are various N substrates for soil N₂O emission because soil nitrification and denitrification are complex processes. Soil ammonium and organic N are critical for soil nitrification at the global scale (Li *et al.* 2020) since they particulate autotrophic nitrification and heterotrophic nitrification, respectively. Soil nitrate is important for denitrification because the nitrate is the substrate of nitrate reductase in the first step of denitrification. It is imperative to test the roles of different soil N substrates on soil N₂O emission at a global scale.

In this study, we compiled the available data from field measurements on soil N₂O emission (6016 observations from 219 articles) across typically terrestrial ecosystems (croplands, forests, grasslands, and wetlands). The specific questions addressed in this study were: 1. What are the global patterns of soil N₂O emission rate

across terrestrial ecosystems? 2. How do climatic factors, soil physical and chemical properties, soil carbon, soil N substrates, microbial characteristics influence soil N₂O emission rate at a global scale? And 3. Which factors are the main drivers on global soil N₂O emission rate?

Materials and methods

To construct dataset of soil N₂O emission

We compiled data from the published peer-view articles. First, we searched the articles taking advantage of two platform: Web of Science (<http://apps.webofknowledge.com>) and China National Knowledge Infrastructure Database (<http://www.cnki.net>) up to July 20, 2019. The terms to search articles were ‘Nitrous oxide’ OR ‘N₂O’ AND ‘Soil’. We also searched articles using Google Scholar. All searched articles were composited into one file and the duplications of articles were removed, resulting in 2165 papers (1730 papers in English and 435 papers in Chinese). The eligible articles were sifted out following the criteria: 1. Soil N₂O emission was collected in situ; 2. The experiment lasted more than two days where the initial measurements were removed from dataset to eliminate the impacts of experimental disturbance; 3. There were unambiguous units for soil N₂O emission rate; 4. The dataset did not include the N₂O emission from water (*e.g.* river sediments or lake sediments). It remained 219 articles after sifting to construct the dataset of soil N₂O emission.

The site-specific information were also distilled from articles, such as the geographic coordinates (*i.e.* latitude and longitude for experimental site), climatic variables (*e.g.* mean annual temperature and mean annual precipitation), soil physical and chemical properties (*e.g.* the contents of sand/clay, soil bulk density, pH, cation exchange capacity, soil moisture by weight). The content of soil C and N (*e.g.* soil organic C, total soil N, dissolved soil organic C, dissolved organic N, available phosphorus, ammonium, nitrate, and the ratio of C to N) and soil microbial biomass (*i.e.* microbial biomass carbon (MBC), MBN, and MBC:MBN) also came from articles. The replicates of experiment were also extracted from articles.

Data overview

The dataset of soil N₂O emission rate from field experiments were constructed on the basis of 219 articles, which included 6016 observations. The dataset of soil N₂O emission rate covered all continents but Antarctica (Figure S1) and the dataset mainly encompassed four ecosystem types. Specifically, 4356 observations came from croplands, 679 observations from forests, 335 observations from grasslands, 394 observations from wetlands, and 252 observations from unclassified ecosystems. The climatic factors and soil properties covered a large scope. For example, the mean annual precipitation ranged from 95 to 4395 mm; the clay content was from 0.3 to 90%; and soil pH varied from 3.08 to 8.77.

Data analyses

All soil N₂O emission rate unified units into $\mu\text{g N m}^{-2} \text{ day}^{-1}$. The averaged soil N₂O emission rate of each ecosystem type/climate zone were calculated and compared using ANOVA approach. The post hoc were tested using ‘*TukeyHSD*’. All statistical analyses were conducted with ‘*stats*’ package.

The relationships between soil N₂O emission rate and environmental factors (*e.g.* climatic factors, soil physical and chemical properties, the contents of soil C and nutrients, and microbial biomass) were tested using linear mixed-effect models. In general, the formula was:

$$\ln(N_2O \text{ emission rate}) = \beta_0 + \beta_1 \times \ln X + \pi_{\text{study}} + \varepsilon \quad (1)$$

where β_0 , β_1 are the intercept and slope value, and π_{study} , ε are the random effect and sampling error, X is the environmental factor, respectively. The random effect, ‘study’, could consider the autocorrelation among observations within the same article.

The structural equation models were used to test the multivariable relationships between soil N₂O emission rate and environmental factors. Initially, we structured the concept models according to the bivariable relationships between soil N₂O emission rate and climatic factors, soil physical and chemical properties, the

contents of soil C and nutrients, as well as microbial biomass. There were direct effects from environmental factors on soil N₂O emission rate and indirect effects that climatic factors, soil properties, and the substrates influenced soil N₂O emission rate through changing soil microbial biomass. The environmental factors (*e.g.* climatic factors, soil physical and chemical properties, soil N contents, and microbial biomass) were viewed as the fixed effects, the ‘study’ was the random effect, and the replicates were ‘weight’ in each structural equation model. Initially, all environmental factors were incorporated into structural equation models, however, the models were not acceptable. The structural equation models were tested by reducing the number of variables one by one. Finally, the optimal models were presented with the lowest Fisher value (1.2) and Akaike information criterion value (35.1). The structure equation models were conducted using ‘*piecewiseSEM*’ package. The redundant variables were omitted in the final structure equation models. For example, the mean annual precipitation did not significantly influence soil N₂O emission rate and microbial biomass when soil moisture was incorporated into models, so we removed mean annual precipitation from models.

To test whether the multiple relationships were robust, we separately conducted analyses in each ecosystem. Although the structural equation model cannot be applied in ecosystem without enough data (*e.g.* wetlands), we normalized all data (Z-score normalization) and factored out the weighted slope in each ecosystem. To get a robust weighted slope, the bivariate relationship was removed while the number of observations was less than 20.

Results

The global patterns of soil N₂O emission rate

The averaged soil N₂O emission rate was 1111.79 (SE = 26.59, N = 6016) $\mu\text{g N m}^{-2} \text{day}^{-1}$ across terrestrial ecosystems (Figure 1a), with large variation between different ecosystem types. The soil N₂O emission rate was the highest in wetlands ($1433.47 \pm 121.75 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 394) but lowest in grassland ($857.64 \pm 77.89 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 335). Croplands had significantly larger soil N₂O emission rate ($1099.02 \pm 31.85 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 4356) than forests ($850.05 \pm 64.56 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 679). There were no significant differences in soil N₂O emission rate between forests and grasslands ($p = 0.99$).

Among climate zones, humid subtropical climate zone had the greatest soil N₂O emission rate ($1424.80 \pm 116.84 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 454) (Figure 1b). Similarly, the soil N₂O emission rate was high under tropical climate ($1023.99 \pm 144.74 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 177) and temperate oceanic climate ($1257.39 \pm 52.61 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 1337). There were no significant differences among tropical climate, monsoon-influenced humid subtropical climate, and temperate oceanic climate. The smallest N₂O emission was observed under semi-arid climate ($188.33 \pm 15.71 \mu\text{g N m}^{-2} \text{day}^{-1}$, N = 241).

Bivariate relationships of soil N₂O emission rate with environmental factors

Soil N₂O emission rate significantly increased with mean annual temperature (slope = 0.73, $p = 0.002$, N = 5404) (Figure 2a), and slightly increased with mean annual precipitation (slope = 0.20, $p = 0.11$, N = 5435, Figure 2b). Soil physical and chemical properties also significantly influenced soil N₂O emission rate at a global scale (Figures 2c-h). Specifically, soil N₂O emission rate decreased with higher soil bulk density (slope = -0.85, $p < 0.001$, N = 1828), and significantly increased with higher soil pH (slope = 0.10, $p = 0.02$, N = 4491), cation exchange capacity (slope = 0.57, $p < 0.001$, N = 343), and soil moisture (slope = 0.70, $p < 0.001$, N = 993). Soil N₂O emission rate tended to increase with soil clay contents (N = 2899), but the relationship was not significant ($p = 0.09$). Soil N₂O emission rate did not significantly change with soil sand content ($p = 0.32$, N = 2705).

Soil N substrates, carbon, and phosphorus influenced soil N₂O emission rate at a global scale (Figure 3). Soil organic matter could promote N₂O emission. For instance, soil N₂O emission rate increased with greater soil organic C (slope = 0.40, $p < 0.001$, N = 4008), total soil N (slope = 0.52, $p < 0.001$, N = 3455), soil dissolved organic N (slope = 0.81, $p < 0.001$, N = 237), while there were no significant relationship between soil N₂O emission rate and soil dissolved organic C (slope = 0.01, $p = 0.92$, N = 612). Soil N₂O emission rate

decreased against the higher soil C:N ratio ($p < 0.001$, $N = 3385$). More soil available phosphorus was likely to increase soil N_2O emission (slope = 0.61, $p < 0.001$, $N = 911$). Soil inorganic N contents also influenced N_2O emission rate, that is, soil N_2O emission rate significantly accelerated with greater concentrations of soil ammonium (slope = 0.27, $p < 0.001$, $N = 2479$) and nitrate (slope = 0.37, $p < 0.001$, $N = 2919$) at a global scale.

Soil microbial biomass influenced soil N_2O emission rate as well (Figure 4). Specifically, soil N_2O emission rate increased with greater soil MBC (slope = 0.29, $p = 0.03$, $N = 449$) and MBN (slope = 0.48, $p < 0.001$, $N = 342$). The soil N_2O emission rate decreased with higher ratio of MBC:MBN at a global scale (slope = -0.49, $p = 0.04$, $N = 231$).

Multivariable relationships between soil N_2O emission rate and environmental factors

The contents of soil nitrate, ammonium, total soil N, MBN, mean annual temperature and soil moisture directly influenced soil N_2O emission rate in structural equation models at a global scale (Figure 5). Among these factors, the N substates (*i.e.* nitrate, ammonium, total N) played the most important role in determining soil N_2O emission rate. Specially, the greater concentrations of soil nitrate significantly accelerated soil N_2O emission rate with the standard coefficient of 0.21 ($p < 0.001$). Moreover, soil N_2O emission rate increased with greater concentrations of total soil N (standard coefficient = 0.13, $p < 0.001$) and ammonium (standard coefficient = 0.11, $p < 0.001$). The joint direct effects (combined standard coefficient = 0.45) of soil nitrate, ammonium, and total soil N accounted for more than half of total direct effects (total standard coefficient = 0.84). Among climatic factors and soil physical/chemical properties, mean annual temperature (standard coefficient = 0.18, $p < 0.001$) and soil moisture (standard coefficient = 0.17, $p < 0.001$) play equivalent roles to drive the changes of soil N_2O emission rate.

Soil N substates and soil properties also influenced soil N_2O emission rate indirectly *via* changing soil microbial biomass in the structural equation models. For example, although soil pH did not directly influence soil N_2O emission rate (standard coefficient = 0.04, $p = 0.14$), higher soil pH could increase soil MBN (standard coefficient = 0.09, $p < 0.001$) which subsequently promoted soil N_2O emission rate (standard coefficient = 0.04, $p < 0.001$). Moreover, soil MBN increased with greater soil ammonium (standard coefficient = 0.09, $p < 0.001$) and soil moisture (standard coefficient = 0.10, $p < 0.001$), and soil MBN was likely to augment with greater total soil N (standard coefficient = 0.003, $p = 0.66$), and then greater soil MBN promoted soil N_2O emission rate.

Together, mean annual temperature, soil moisture, pH, MBN, and soil N substrates accounted for 40% variations of soil N_2O emission. The concentrations of soil N substrates dominated the variations of soil N_2O emission rate (total standard coefficient = 0.45) in comparison with soil moisture (total standard coefficient = 0.19) and mean annual temperature (total standard coefficient = 0.18) at a global scale.

Bivariate relationships of soil N_2O emission rate with environmental factors in different ecosystems

The soil N_2O emission rate pervasively correlated with the concentrations of soil nitrate (weighted slope = 0.36 in croplands, 0.36 in forests, 0.30 in grasslands, and 0.27 in wetlands, respectively) and ammonium (weighted slope = 0.26 in croplands, 0.25 in forests, 0.27 in grasslands, and 0.27 in wetlands, respectively) in each ecosystem type (Figure 6). Soil N_2O emission rate also positively correlated with the concentrations of total soil N in each ecosystem (weighted slope = 0.19 in croplands, 0.24 in forests, and 0.35 in grasslands, respectively) except for wetlands (weighted slope = 0.04, $p = 0.81$). In addition, soil N_2O emission rate positively related to MBN in croplands (weighted slope = 0.17) and forests (weighted slope = 0.20). Soil moisture played an important role in determining soil N_2O emission rate in croplands (weighted slope = 0.18), forests (weighted slope = 0.30), and grasslands (weighted slope = 0.41), whereas the relationship was insignificant in wetlands ($p = 0.11$). The soil N_2O emission rate did not show consistent relationships with other environmental factors across ecosystem types. For example, there were significantly positive relationships between soil N_2O emission rate and mean annual temperature in croplands and forests rather than in grasslands ($p = 0.38$) and wetlands ($p = 0.72$). Soil N_2O emission rate significantly positively related to mean annual precipitation in forests and grasslands rather than in croplands ($p = 0.86$) or wetlands ($p =$

0.35).

Discussion

This study uncovers the general patterns and controlling factors of soil N₂O emission rate at a global scale. The soil N substrates (*i.e.* nitrate, ammonium, and soil organic N) accounted for the most variations of soil N₂O emission in comparison with climatic factors and soil physical and chemical properties. The global synthesis enables us to reconcile controversial viewpoints on the controlling factors on soil N₂O emissions and set a benchmark to evaluate nitrogen cycling models.

The main drivers of soil N₂O emission rate at a global scale

Soil N substrates (*i.e.* nitrate, ammonium, and total soil N), microbial biomass, soil moisture, and mean annual temperature are the drivers of N₂O emission rate across terrestrial ecosystems. Among them, the N substrates are the most important controlling factors on soil N₂O emission rate at a global scale, which is contrast to previous studies that found soil pH is the chief controller of soil N₂O emission at the global scale while soil substrates were not considered (Wang *et al.* 2018b). High soil pH promotes N mineralization (Li *et al.* 2019) and increases MBN (Figure 5 and (Li *et al.* 2020)) which subsequently facilitates N₂O emission. However, when we considered the role of soil N substrates, soil pH played a less important role for predicting N₂O emission (Figure 5). The great soil nitrate availability promotes denitrification and therefore increases N₂O emission. There are some reasons for that soil nitrate is important for N₂O emission. Soil nitrate is the reactant for denitrification. The denitrifier activity positively correlates with nitrate contents (Enwall *et al.* 2010). Moreover, soil denitrification enzyme activity is higher in soils with more nitrate (Gardner & White 2010). For example, soil denitrification enzymatic activity increases from 0.02 mg N kg⁻¹ h⁻¹ to 11.6 mg N kg⁻¹ h⁻¹ under nitrate additions in some wetlands (White & Reddy 1999). Additionally, higher soil nitrate increases the ratio of N₂O to N₂ during denitrification (Senbayram *et al.* 2012). For instance, N₂O:N₂ increases from 19% under 10 mg N kg⁻¹ to 59% under 100 mg N kg⁻¹ (Wang *et al.* 2013).

Soil ammonium and soil total N (almost in organic form) also significantly impact soil N₂O emission. Great soil ammonium level increases ammonia-oxidizing bacteria abundance (Tian *et al.* 2014) that can promote soil autotrophic nitrification. For example, soil N₂O emission increases from 238-277 g N ha⁻¹ yr⁻¹ to 853-1301 g N ha⁻¹ yr⁻¹ when the aqua ammonia applies from 0 to 260 kg ha⁻¹ (Pittelkow *et al.* 2013).

Soil organic N is the substrate of heterotrophic nitrification. In some cases, soil heterotrophic nitrification accounts for 7-19% of total nitrification (Islam *et al.* 2007) and even more than 50% of the total nitrification in acid soil condition (Liu *et al.* 2015). Moreover, soil organic N can increase soil microbial biomass and subsequently increase N mineralization (Li *et al.* 2019). A recent study revealed that the content of soil total N is the main driver for soil nitrification rate at the global scale (Li *et al.* 2020). In line with our finding, a recent study revealed that manure application also substantially increases N₂O emission by 5.1-58.2% (Zhou *et al.* 2017). The key role of soil N contents on soil N₂O emission was also confirmed by the consistently positive relationships between soil N₂O emission rate and soil nitrate, ammonium, and total soil N in each ecosystem type (Figure 6).

Soil moisture influences soil N₂O emission directly and also indirectly through changing soil microbial biomass (Figure 5). Soil moisture regulates N₂O emission possibly through the availability of substrates and the microbial activity. Soil with low moisture hampers the diffusion of soil N substrates to microbial cells (Stark & Firestone 1995). Soil moisture can influence the dynamics of soil microbial biomass, *e.g.* the higher soil moisture promoting soil MBN by 56.3-91.4% in dry ecosystems (Huang *et al.* 2018). Moreover, at low soil moisture microbial cell dehydration occurs which lowers the activity of nitrifying bacteria (Stark & Firestone 1995). Thus, the efficiency of soil processes are stimulated under higher soil moisture (Zhang *et al.* 2019b). Finally, soil moisture can alter soil nitrification and denitrification where both processes can produce N₂O (Bollmann & Conrad 1998). In some cases, more N₂O emission comes from denitrification at a soil moisture more than 70%, in which N₂O emitted 1 to 412 mg N m⁻² per 15 days when soil moisture increased from 40 to 90% (Ruser *et al.* 2006). The important role of soil moisture on N₂O emission is also manifested that it is the important predictor of the temperature sensitivity (Q_{10}) of N₂O emission in an alpine meadow

ecosystem (Zhang *et al.* 2020).

Higher temperature can stimulate the activity of microbes and subsequently influences soil N₂O emission. High temperature stimulates the activities of nitrifier and denitrifier. A recent study showed that the assimilation of ¹³CO₂ by ammonia-oxidizing archaea (one type of autotrophic nitrifier) increases when soil temperature is elevated by 3°C (Hu *et al.* 2016). Similarly, warming (+ 3.6°C) enhances nirS-type denitrifiers by 38%, nirK-type denitrifiers by 82% (Qu *et al.* 2018), and norB-type denitrifier by 4.32% (Zhou *et al.* 2012). In some meadow ecosystem with higher soil moisture, the changes of temperature can explain up to 35% variations of annual soil N₂O flux (Hu *et al.* 2010).

Implications for soil N₂O emission under global change

Fertilization is a common management in croplands, which can dramatically increase soil nitrate and ammonium concentrations that will promote soil N₂O emission. As reported, the rise of N₂O emission is mainly ascribed to accelerating usage of synthetic N fertilizers after 1960 (Davidson 2009). A recent study revealed that the amount of N into croplands under the current fertilization far exceeds the capacity of crop uptake, because crop only uptake about 48.5 kg N ha⁻¹ while the amount of N fertilization is 240 kg N ha⁻¹ (Chen *et al.* 2017). The surplus N fertilization may lose in the form of N₂O. A meta-analysis reported soil N₂O emission increases by 90% under N application at 50-100 kg N ha⁻¹ and the N₂O emission increases by up to 262% under N application at 250-300 kg N ha⁻¹ in croplands (Sun *et al.* 2016). In addition, the fertilization does not only enhance soil N₂O emission in croplands, but impact soil N₂O emission of wetlands through runoff. The N is imported into wetlands that will emit in the form of N₂O since the N₂O emission rate are also sensitive to nitrate/ammonium in wetlands (Figure 6). The higher N₂O emission rate in wetlands (Figure 1) may be caused by the higher N concentrations of runoff from croplands that has increased by 31-46% since 1990 in China (Hou *et al.* 2018). The increasing N concentrations of runoff (Wang *et al.* 2018a) and the higher organic N eventually enhance soil N₂O emission in wetlands. In the late century, the N application in croplands increase substantially in the form of synthetic N (Yu *et al.* 2019a), in some regions the amount of N application has been up to 550-600 kg N ha⁻¹ yr⁻¹ (Ju *et al.* 2009). To meet the growing food requirement, the fertilizer inputs will not decrease in the next century (Erisman *et al.* 2008), therefore, soil N₂O emission will correspondingly increase under growing fertilization in the near future.

Nitrogen deposition also increases soil N₂O emission. Soil N₂O emission is increased by 91.3% (Deng *et al.* 2020) and 215% (Liu & Greaver 2009) under N deposition at the global scale. High N deposition increased the N₂O flux where average annual N₂O fluxes increased by 13.7% at 7 kg N ha⁻¹ yr⁻¹, 47.6% at 20 kg N ha⁻¹ yr⁻¹, and 98.7% at 40 kg N ha⁻¹ yr⁻¹, respectively (Yan *et al.* 2018). In the last four decades, global N deposition increases by 8% (Ackerman *et al.* 2019), and the N deposition still is the critical question on earth, for example, N deposition (*i.e.* NH_x and NO_x) amounts up to 19.6 – 20.4 kg N ha⁻¹yr⁻¹ in China (Yu *et al.* 2019b). Although N deposition can contribute to global greening (by 9%) (Zhu *et al.* 2016), the role of N deposition on N₂O emission should also be paid more attentions.

Warming will increase soil N₂O emission as well. The previous experimental studies showed that warming can stimulate soil N₂O emission and the rate of increase is very steep when soil denitrification is the dominant process (Smith 1997). A recent study revealed warming significantly increases soil N₂O emission when soil N substrates is adequate (Zhang *et al.* 2020), indicating that warming may enhance soil N₂O emission in croplands with fertilization.

Implications for ecosystem modeling

The dataset and the findings in this study can facilitate modeling study of soil N₂O emission. First, this study compiled a big data (*i.e.* 6016 observations) of soil N₂O emission from field across main terrestrial ecosystem types to provide benchmark for model evaluation. Second, the data can be helpful to calibrate process-based model, for instance, Dynamic Land Ecosystem Model (DLEM) calculates soil N₂O emission on the basis of nitrification and denitrification processes primarily based on soil N substrates, temperature, and soil moisture (Xu *et al.* 2017). Our data can be useful for calibrating parameters of models. Third, the findings in this study that N substrates are critical for soil N₂O emission across terrestrial ecosystems will

offer insights for model development. For example, soil organic N and MBN significantly influence soil N₂O emission at the global scale, particularly in croplands, forests, and grasslands. Moreover, a recent study also revealed that soil organic N can explain the most variations of soil nitrification at the global scale (Li *et al.* 2020). However, most land models in predicting soil N₂O have not considered the roles of soil organic N and MBN (Tian *et al.* 2018). Thus, incorporating soil N substrates and MBN may reduce the model uncertainty in projection of soil N₂O emission.

Uncertainties and limitations

There are some uncertainties in this synthesis. First, climatic factors, soil physical and/or chemical properties, the concentrations of substrate can influence soil N₂O emission through changing soil microbial biomass or the activities of microbes. Although we verified that soil substrates and soil properties affect soil N₂O emission rate *via* MBN (Figure 5), we did not test the effects of the microbial activities because of data paucity. In nitrification and denitrification, there are many functional genes expressing enzymes to participate the specific processes. For instance, ammonia-oxidizing bacteria and ammonia-oxidizing archaea mediate the first step of soil nitrification, and the community dynamics may be important for nitrification (Theodorakopoulos *et al.* 2017). Therefore, the roles of functional microbes on soil N₂O emission remain to be tested at a global scale. Second, soil moisture may play roles on soil N₂O emission *via* altering soil redox potential (Rubol *et al.* 2012) other than soil microbial biomass. We did not compile enough data of redox potential to test in this study. Third, the data mainly came from croplands (72.4%). Although the relationships between soil N₂O emission and environmental factors were similar in other ecosystem types (Figure 6), the variations of weighted slope were obviously larger when the number of observations was small in wetlands.

This study revealed the comprehensive patterns of and identified controlling factors on soil N₂O emission rates at the global scale. Although climatic factors (*e.g.* mean annual temperature), soil physical and chemical properties (*i.e.* soil pH, bulk density, and soil moisture) significantly influenced soil N₂O emission, soil N substrates (*i.e.* soil nitrate, ammonium, and total soil N) accounted for the most variations in soil N₂O emission rates at the global scale. The critical roles of soil N contents in soil N₂O emission were confirmed by the consistently significantly positive relationships between soil N₂O emission rates and the contents of soil nitrate, ammonium, and total soil N across ecosystem types. The findings highlight the necessity that soil N substrates (*i.e.* nitrate, ammonium, and total soil organic N) should be comprehensively incorporated into models to improve the projection accuracy of soil N₂O emission at the global scale.

Data Accessibility

Data supporting the results are found in supplementary.

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Author contributions

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

Competing interests

The authors declare no competing financial interests

Figure legends

Figure 1

The changes of soil N₂O emission rate with ecosystems (a) and climate zones (b). The green bars are standard error and the white values are the numbers of observations in ecosystems. The abbreviation of UE stands for unclassified ecosystem (a). The climate zones were classified according to Koppen Climate Classification. Cwa is Monsoon-influenced humid subtropical climate. Cfa is Humid subtropical climate. Cfb is Temperate oceanic climate. Af, Am, and Aw are Tropical rainforest climate, Tropical monsoon climate, and Tropical wet and dry climate, respectively. Dfb is Warm-summer humid continental climate. Dfa is Hot-summer humid continental climate. Dwa and Dwb are Monsoon-influenced hot-summer humid continental climate and Monsoon-influenced warm-summer humid continental climate, respectively. BSh and BSk are Hot semi-arid climate and Cold semi-arid climate, respectively. The average soil N₂O emission rate of climate zone

with the observations being more than 100 was presented (b). The different letters above bars indicate significantly different soil N₂O emission rate.

Figure 2

The bivariate relationships between soil N₂O emission rate and mean annual temperature (MAT, a), mean annual precipitation (MAP, b), soil sand content (c), clay content (d), bulk density (BD, e), pH (f), cation exchange capacity (CEC, g), and soil moisture (h) at a global scale using the logarithmically transformed data. The green lines with grey shadings are the slopes \pm 95% confidence intervals. The size of circles is the number of replicates from 1 to 60. The number without parentheses is the number of observations and the number with parentheses is for studies.

Figure 3

The bivariate relationships between soil N₂O emission rate and carbon and nitrogen, namely, the content of soil organic carbon (SOC, a), soil nitrogen (TN, b), the ratio of soil carbon to nitrogen (soil C:N, c), soil dissolved organic carbon (DOC, d), soil dissolved organic nitrogen (DON, e), available phosphorus (AP, f), the concentration of soil ammonium (NH₄⁺-N, g), and soil nitrate (NO₃⁻-N, h) at a global scale using the logarithmically transformed data. The green lines with grey shadings are the slopes \pm 95% confidence intervals. The size of circles is the number of replicates from 1 to 60. The number without parentheses is the number of observations and the number with parentheses is for studies.

Figure 4

The bivariate relationships between soil N₂O emission rate and soil microbial characteristics, namely, microbial biomass carbon (MBC, a), microbial biomass nitrogen (MBN, b), and the ratio of microbial biomass carbon to microbial biomass nitrogen (MBC:MBN, c) at a global scale using the logarithmically transformed data. The green lines with grey shadings are the slopes \pm 95% confidence intervals. The size of circles is the number of replicates from 1 to 60. The number without parentheses is the number of observations and the number with parentheses is for studies.

Figure 5

The multiple relationships of soil N₂O emission rate at the global scale. The orange lines are the significantly positive relationships, blue lines are the significantly negative relationships, and the green dashed lines are the insignificant relationships, in which the statistically significant level is α [?] 0.05. Numbers are standardized coefficients. MAT, SM, TN, and MBN represent mean annual temperature, soil moisture, total soil nitrogen, and microbial biomass nitrogen, respectively.

Figure 6

The slopes of the bivariate relationships between soil N₂O emission rate and MAT (mean annual temperature), MAP (mean annual precipitation), Sand, Clay, BD (bulk density), pH, CEC (cation exchange capacity), Moisture, SOC (soil organic carbon), TN (total soil nitrogen), soil C:N, DOC (soil dissolved organic carbon), DON (dissolved organic nitrogen), AP (available phosphorus), NH₄-N, NO₃-N, MBC (soil microbial biomass carbon), MBN (microbial biomass nitrogen), MBC:MBN across terrestrial ecosystems. The blue dot is averaged slope and the bars are 95% confidence intervals. The values in parentheses are the number of studies and values without parentheses are the number of observations.

Figure 1

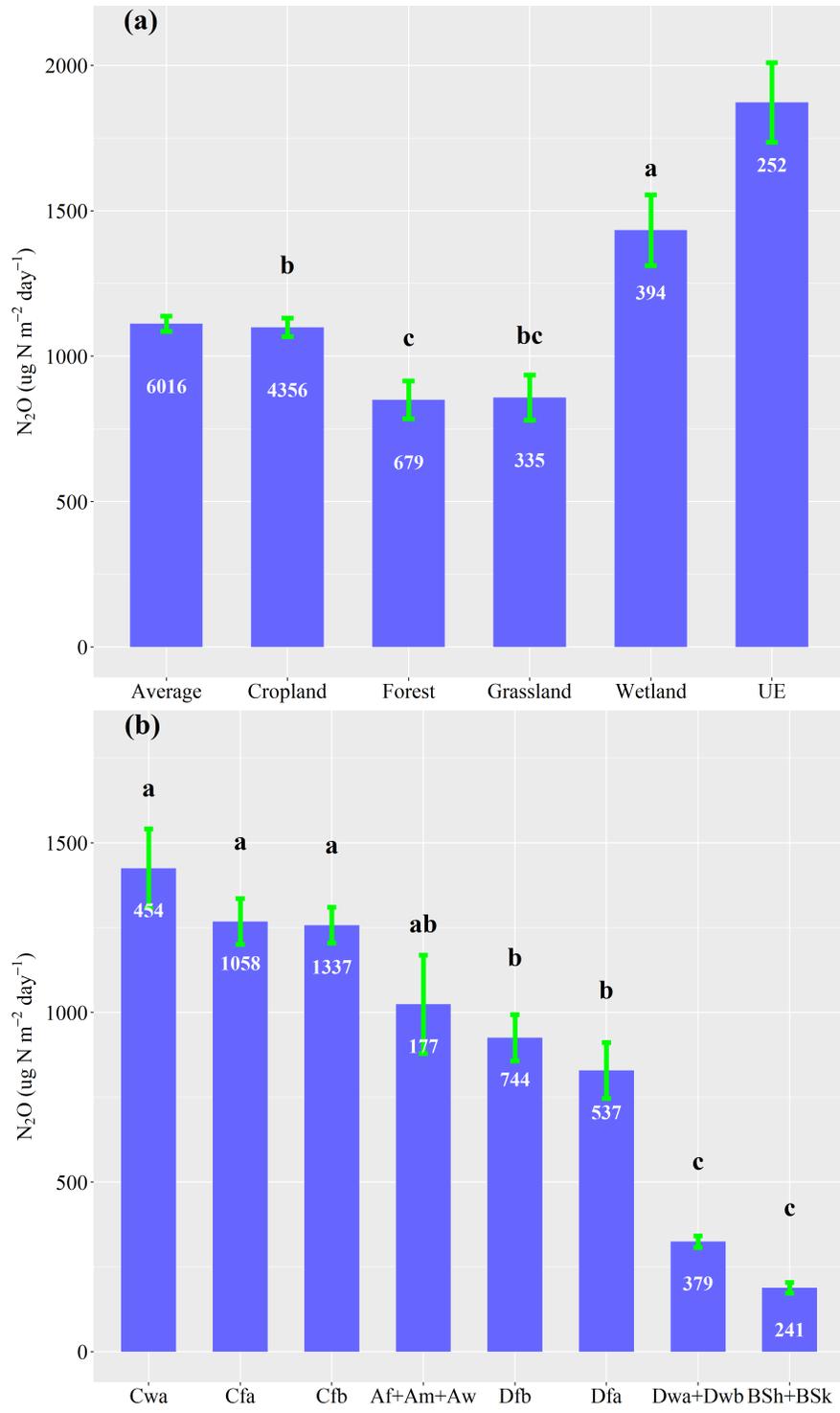


Figure 2

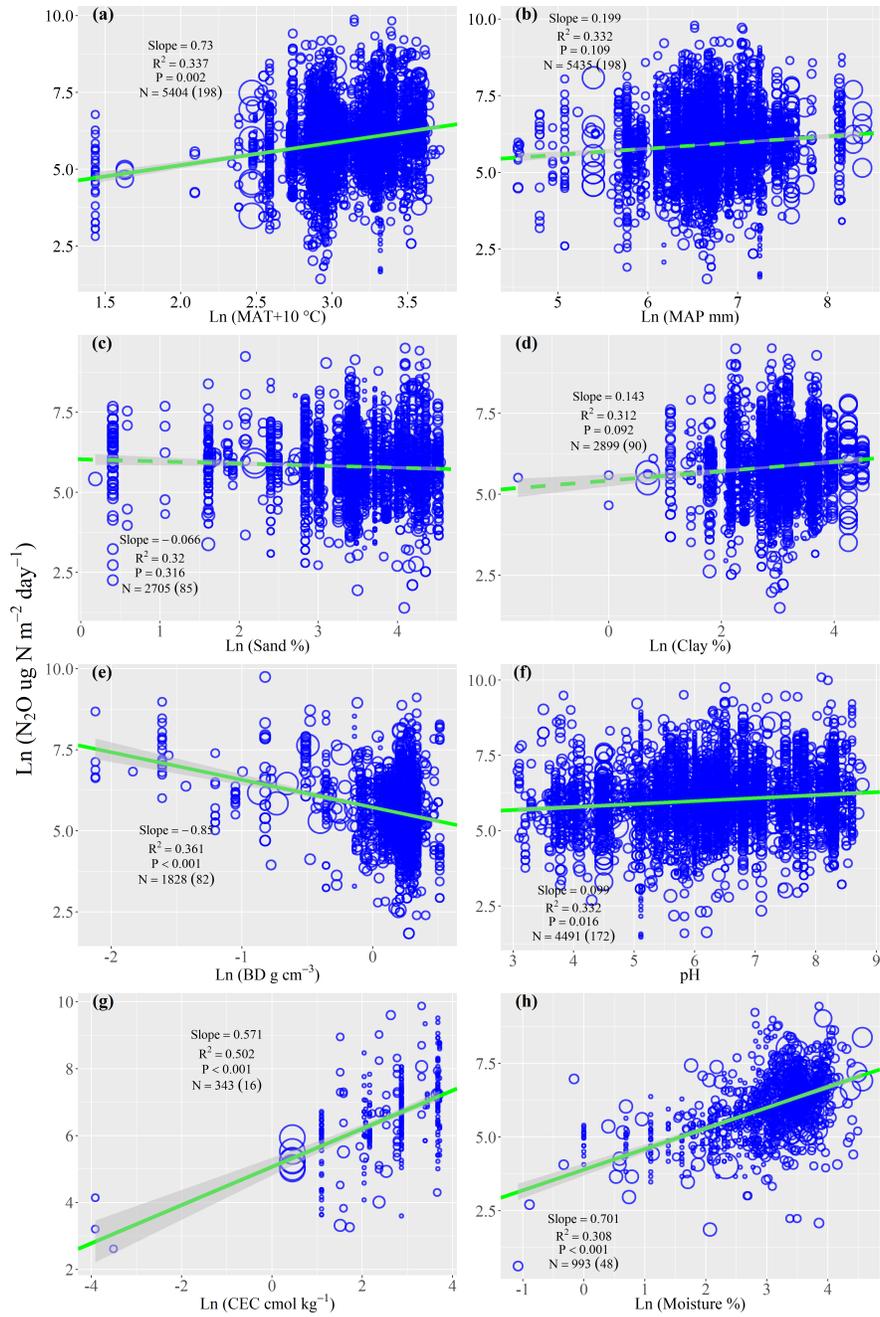


Figure 3

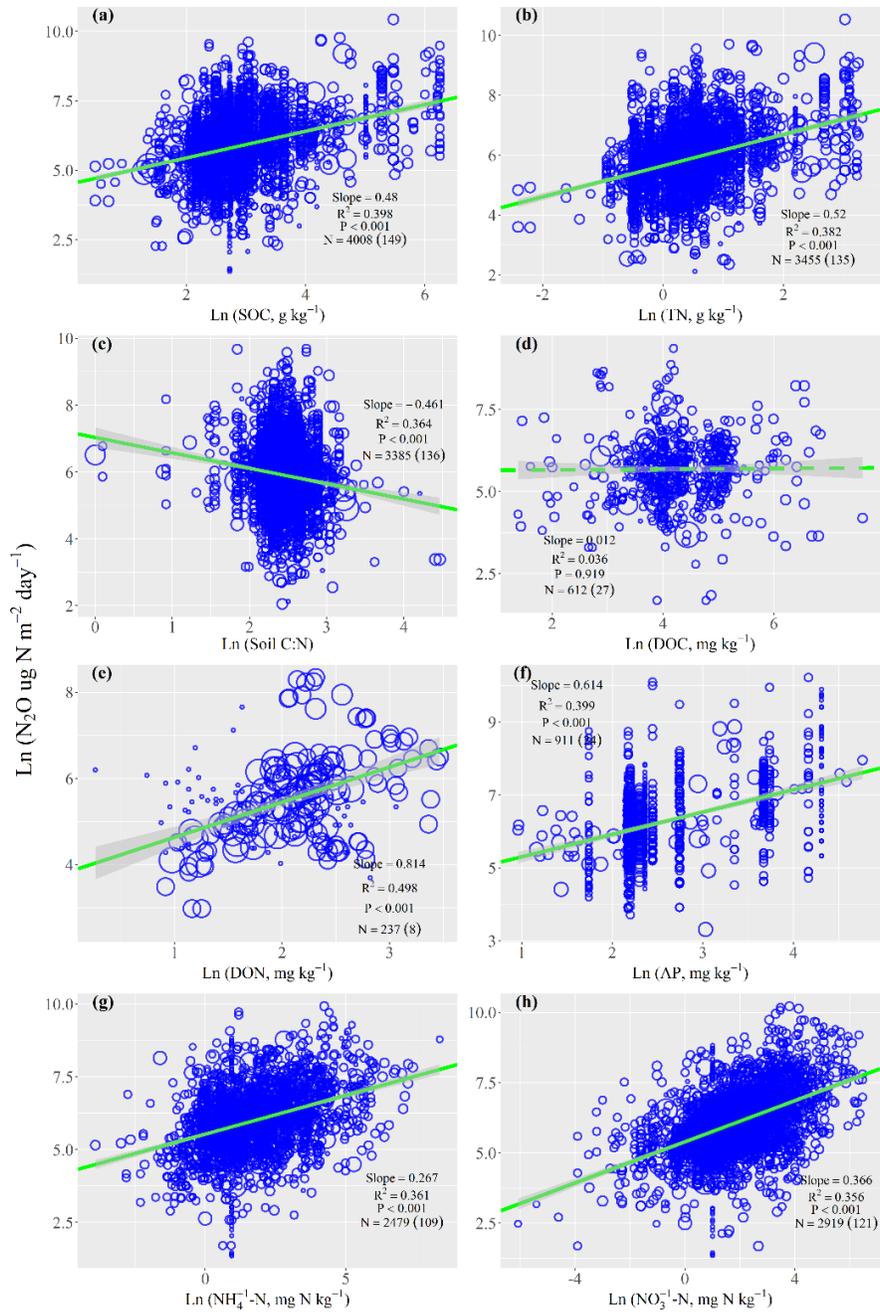


Figure 4

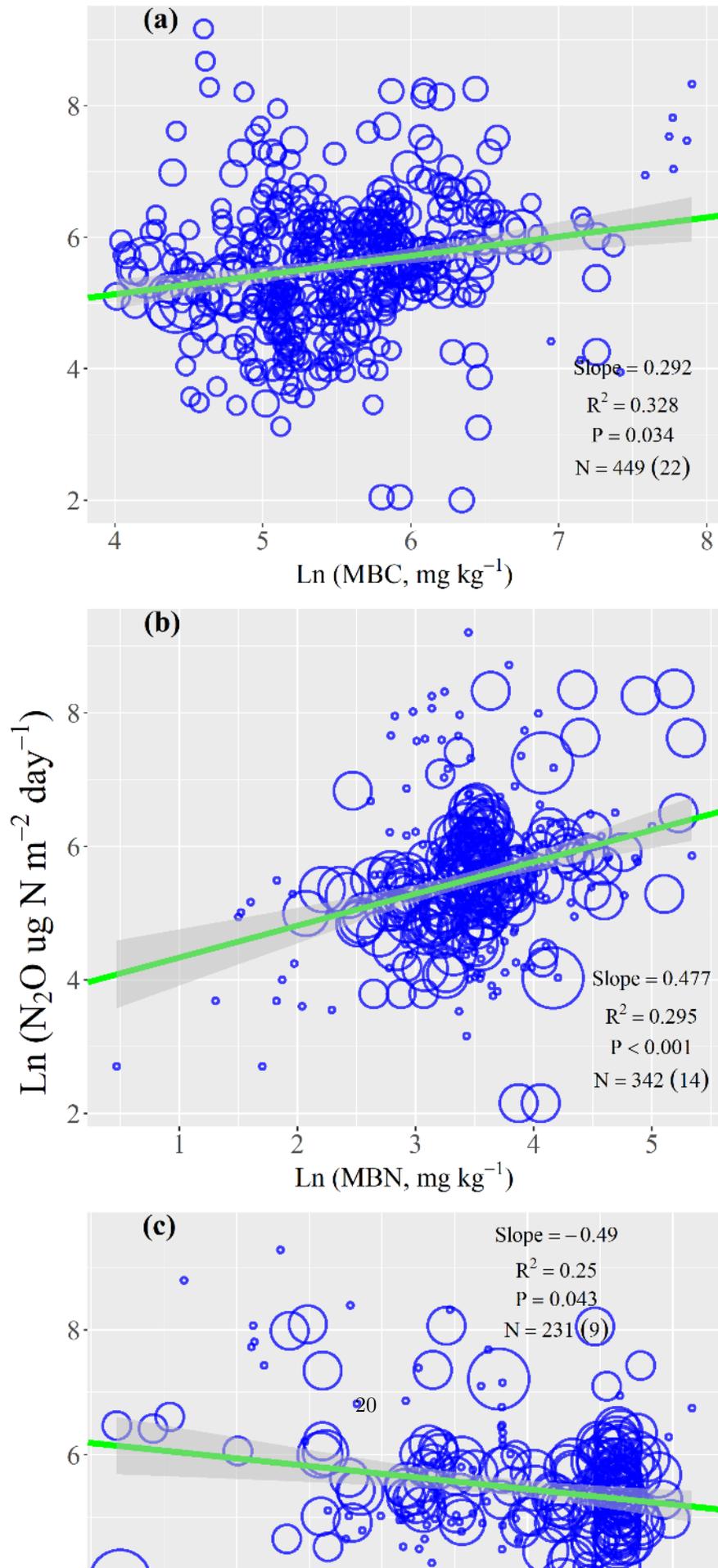


Figure 5

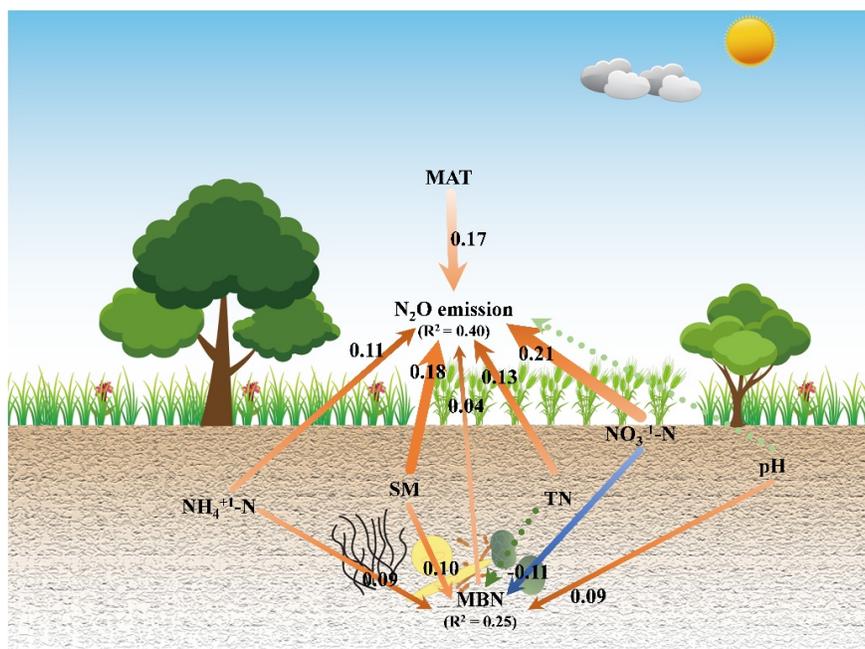


Figure 6

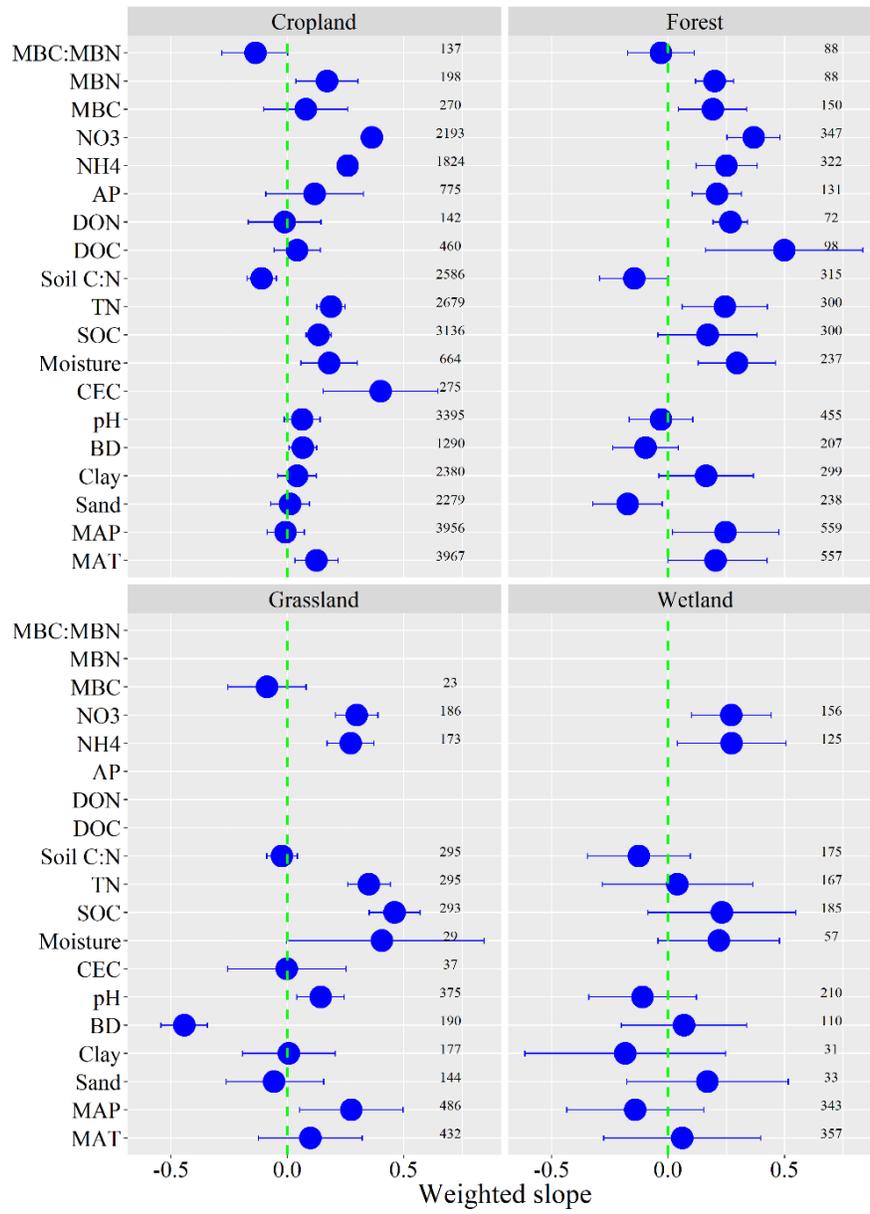


Figure S1

Global distribution of field data on soil N₂O emission rates in this study

