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Variations and controlling factors of soil denitrification rate

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Abstract

The denitrification process profoundly affects soil nitrogen (N) availability and generates its byproduct, nitrous oxide, as a potent greenhouse gas. There are large uncertainties in predicting global denitrification because its controlling factors remain elusive. In this study, we compiled 4301 observations of denitrification rates across a variety of terrestrial ecosystems from 214 papers published in the literature. The averaged denitrification rate was 3516.3 ± 91.1 μg N kg^{-1} soil day^{-1}. The highest denitrification rate was 4242.3 ± 152.3 μg N kg^{-1} soil day^{-1} under humid subtropical climates, and the lowest was 965.8 ± 150.4 μg N kg^{-1} under dry climates. The denitrification rate increased with temperature, precipitation, soil carbon and N contents, as well as microbial biomass carbon and N, but decreased with soil clay contents. The variables related to soil N contents (e.g., nitrate, ammonium, and total N) explained the variation of denitrification more than climatic and edaphic variables (e.g., mean annual temperature (MAT), soil moisture, soil pH, and clay content) according to structural equation models. Soil microbial biomass carbon, which was influenced by soil nitrate, ammonium, and total N, also strongly influenced denitrification at a global scale. Collectively, soil N contents, microbial biomass, pH, texture, moisture, and MAT accounted for 60% of the variation in global denitrification rates. The findings suggest that soil N contents and microbial biomass are strong predictors of denitrification at the global scale.

KEYWORDS
fertilization, global warming, microbes, nitrogen cycling, soil denitrification

1 | INTRODUCTION

Denitrification is an important process in nitrogen (N) cycling that transforms reactive N (e.g., nitrate) to inert N (i.e., N_2) and affects N availability in ecosystems. It can reduce the active nitrogen amount in ecosystems when the nitrate is entirely converted to N_2. Incomplete denitrification process leads to nitrous oxide (N_2O), a potent greenhouse gas that also contributes to stratospheric ozone depletion. The annual denitrification is approximately 330 Tg N in terrestrial ecosystems (Kuypers et al., 2018), and soil is the primary location of denitrification (Groffman, 2012). With the substantial increase in reactive N inputs to ecosystems (Cui et al., 2013), the roles of denitrification in N cycling requires renewed attention as evidence suggests emissions of N_2 and N_2O through denitrification have increased by approximately 74% in the last century (Bouwman et al., 2013). Additionally, anthropogenic activities, such as heavy application of N fertilizer and/or N deposition, will further increase soil N budget (Bouwman et al., 2013); thus, the prediction of denitrification has become an important issue. However, there are large uncertainties in the current projection of denitrification rates, with projections ranging from 72 to 185 Tg N year^{-1} (Bouwman et al., 2013). It is necessary to reveal the controlling factors on denitrification to better estimate soil denitrification at the global scale.

Denitrification is mediated by many factors, including climate, soil physical and chemical properties, and microbes (Martinez-Espinosa et al., 2021; Xu et al., 2013). In general, denitrification rate increases with temperature (Shan et al., 2018) and precipitation (Barnard et al., 2006). Denitrification rate changes substantially during soil wetting-drying (Groffman & Tiedje, 1988) and increases by 0.24–0.55 mg N m^{-3} h^{-1} with soil moisture (SM) ranging from 20 to 40 cm^3 cm^{-3} (Tan et al., 2018b). Soils with high clay content are likely to weaken denitrification (Wang et al., 2018) as they adsorb more nitrate (Mohsenipour et al., 2015). Higher soil pH can stimulate denitrification (Cuhel & Simek, 2011). In addition, the denitrification rate is also regulated by soil carbon and N contents. For example, straw addition substantially stimulates denitrification rate (Pan et al., 2017) because it provides readily available substrates for denitrification. A recent study finds nitrate and carbon additions double the denitrification rate (Li et al., 2018). Soil microbes also contribute significantly to the denitrification rate (Seo & DeLaune, 2010). However, the effects of climatic factors, soil properties, and microbes on denitrification rate are mainly evaluated in case studies and remain untested at larger spatial scales. Two recent reviews on denitrification emphasized the detection of the main controlling factor of denitrification at ecosystem and global scales (Almaraz et al., 2020; Groffman, 2012), whereby the process-based relationships will promote the model of the denitrification.

The denitrification process usually includes conventional denitrification (*sensu stricto* denitrification in some studies), nitrifier denitrification, codenitrification, and chemodenitrification (Wrage et al., 2001). The responses of different denitrification pathways to the same soil property may differ. One study reports that conventional denitrification rate increases with soil pH (from 4.3 to 7.0) (Hall et al., 1998), but there is no significant relationship between nitrifier denitrification and soil pH (Wrage et al., 2004). Another study reveals that the lower pH may motivate nitrifier denitrification from a thermodynamic viewpoint (Wrage et al., 2001). The different responses of various denitrification pathways to a certain soil property will weaken the relationship between total denitrification rate and this soil property. However, all these denitrification pathways eventually depend on their corresponding substrates, so we hypothesized that the combined effect of soil N substrates will dominate the variations in total denitrification rate at a global scale compared to other variables (H_1). Moreover, although soil chemodenitrification is a chemical process using nitrite and ferrous iron (Jones et al., 2015), the other pathways of denitrification are mainly a bio-process carried out by a large range of microorganisms (Hayatsu et al., 2008), such as alpha-, beta-proteobacteria, and Bacteroidetes, etc. (Jones et al., 2013). Soil properties and climatic factors could impact denitrifiers and eventually influence denitrification (Wallenstein et al., 2006). A case study confirms that SM, organic matter, and nitrate changed soil denitrifiers and further influenced denitrification rate (Attard et al., 2011), but this has not been tested at larger spatial scales. We hypothesized that soil microbes are also an important driver for global denitrification rates and that changes in soil properties and climatic factors could indirectly impact denitrification through microbes (H_2).

To reveal the general patterns of denitrification rate at a global scale and to test the above hypotheses, we compiled the available denitrification data from published peer-review articles (4301 observations from 214 articles) across the main terrestrial ecosystems (i.e., croplands, forests, grasslands, and wetlands). In this study, we addressed three specific questions: (1) What are the patterns of denitrification rate across terrestrial ecosystems? (2) How do climatic factors, soil physical and chemical properties, and soil microbes influence denitrification rate at a global scale? (3) Which factors are the main controlling factors of denitrification rate at large spatial scales?

2 | METHODS AND MATERIALS

2.1 | Data compilation

We collected the available denitrification rate from published papers. The screening of articles was conducted using two platforms: Web of Science (http://apps.webofknowledge.com) and China National Knowledge Infrastructure Database (http://www.cnki.net). The keywords used to identify relevant articles were "Denitrification rate" AND "Soil." Additional screening was performed using Google Scholar. Papers were screened up to a publication data of September 10, 2019. For a study to be eligible in our analyses, we required the following criteria: (1) Denitrification was measured using the upper soil, mainly in the top 15 cm of soil (such as 0–15, 0–7.5, and 7.5–15 cm). (2) There are several methods to measure denitrification rate, such as acetylene-based method, direct N_2 quantification, mass balance approaches, molecular approaches, etc. In this study, the denitrification rate was collected from studies using the acetylene-based method, as this is the most commonly used approach in terrestrial ecosystems since the 1970s (Groffman et al., 2006). (3) The denitrification rates were collected generally after the soil incubated for 48 h, when the incubated soil was under relatively stable anerobic condition and the denitrifying enzymes were active (Holtan-Hartwig et al., 2000, 2002). The data set also included the available site-specific information, for example, climatic data and soil properties. The number of experimental replications was also extracted from articles.

2.2 | Data set overview

The data set of denitrification rates includes 4301 observations from 214 peer-reviewed articles, and the data set was reposed at Dryad (Li, 2021). Most observations came from laboratory measurements (2653 observations). The geographical distribution of these observations is shown in Figure S1. The majority of the denitrification rate data came from Asia, North America, and Europe. To be specific, 1398 observations came from Asia, 1184 observations came from North America, 832 observations from Europe, 119 observations from Africa, 28 observations from Australia, 22 from South America, and 718 observations lacked geographic coordinates. The data set encompassed observations from four ecosystem types, namely, croplands (2427), forests (350), grasslands (552), and wetlands (863), with 109 observations lacking a clear ecosystem identifier. The soil properties and climatic factors had large ranges. For example, the clay content ranged from 1.2% to 84%, soil pH ranged from 2.6 to 9.6, mean annual temperature (MAT) ranged from 1.89 to 28°C, and mean annual precipitation (MAP) ranged from 180 to 3457 mm.

2.3 | Data analyses

The unit of denitrification rate were unified to μg N kg^{-1} soil day^{-1} and adjusted to 25°C using a fixed value of Q_{10}, 2.53 averaged from reported Q_{10} (Bonnett et al., 2013; Duan et al., 2019; Hu et al., 2013; Silvennoinen et al., 2008). We calculated the average denitrification rate in each ecosystem type and climate zone. The comparisons of denitrification rate across ecosystem types/climate zones were conducted using ANOVA and the post hoc were conducted using "*TukeyHSD*."

We tested the bivariate relationships of denitrification rate against environmental variables (climatic factors, soil properties, microbial traits, etc.) by virtue of linear mixed-effect models. The equation is:

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

where X is the environmental factor, β_0, β_1 are the intercept and slope value, and π_{study}, ε are the random effect and sampling error, respectively. The random effect, "study," accounted for the autocorrelation of observations within a study.

The multivariable relationships between the denitrification rate and environmental variables were tested using structural equation models. First, we constructed the conceptual structural equation models for denitrification rate based on the bivariate relationships between the denitrification rates and environmental variables. In the conceptual models, climatic factors (MAT, MAP), soil properties [soil clay content, pH, SM, soil carbon and N contents (e.g., total soil nitrogen, TN)], and microbial traits (microbial biomass carbon [MBC], microbial biomass nitrogen [MBN], and MBC:MBN) were predicted to significantly and directly influence the denitrification rate. Furthermore, climatic factors and soil properties might indirectly impact the denitrification rate by altering microbial traits. We tested the conceptual models using the "*piecewiseSEM*" package. Based on the bivariate regressions, any variable with significant effects on denitrification rate was included in the initial structural equation models. The structural equation models were stepwise optimized by reducing redundant variables. The criteria to select optimal models were the minimum Akaike information criterion (AIC) value and a higher p value. For instance, although a significantly bivariate relationship between denitrification rate and MAP was observed, there were no significant relations between denitrification rate and/or microbial biomass and MAP in structural equation models; therefore, MAP was removed in the final structural equation models (AIC = 40.7, $p = .60$).

We also performed analyses to verify whether the multiple relationships were robust in each ecosystem type. Because the number of observations in some ecosystems (e.g., forests) did not match the requirement to conduct structural equation models (e.g., forests), we normalized all data in an individual ecosystem and tested the relationship between denitrification rates and environmental factors using mixed-effect models. We extracted the weighted slope of each relationship and presented them in figures.

3 | RESULTS

3.1 | Denitrification rates across ecosystem types and climate zones

The averaged denitrification rate was 3516.32 ± 91.08 μg N kg^{-1} soil day^{-1} (observation number (Num) = 4301) at a global scale (Figure 1a). The highest denitrification rate was observed in croplands with 4181.71 ± 135.21 μg N kg^{-1} soil day^{-1} (Num = 2427). Forests (3279.65 ± 252.27 μg N kg^{-1} soil day^{-1}, Num = 350) and grasslands (3283.71 ± 255.68 μg N kg^{-1} soil day^{-1}, Num = 552) had similar mean denitrification rates at the global scale, and were significantly lower than that of croplands ($p = .043$, $p = .009$, respectively). There were no significant differences in denitrification rate between forests and grasslands ($p = .99$). The lowest mean denitrification rate was 2086.17 ± 130.61 μg N kg^{-1} soil day^{-1} (Num = 863) in wetlands.

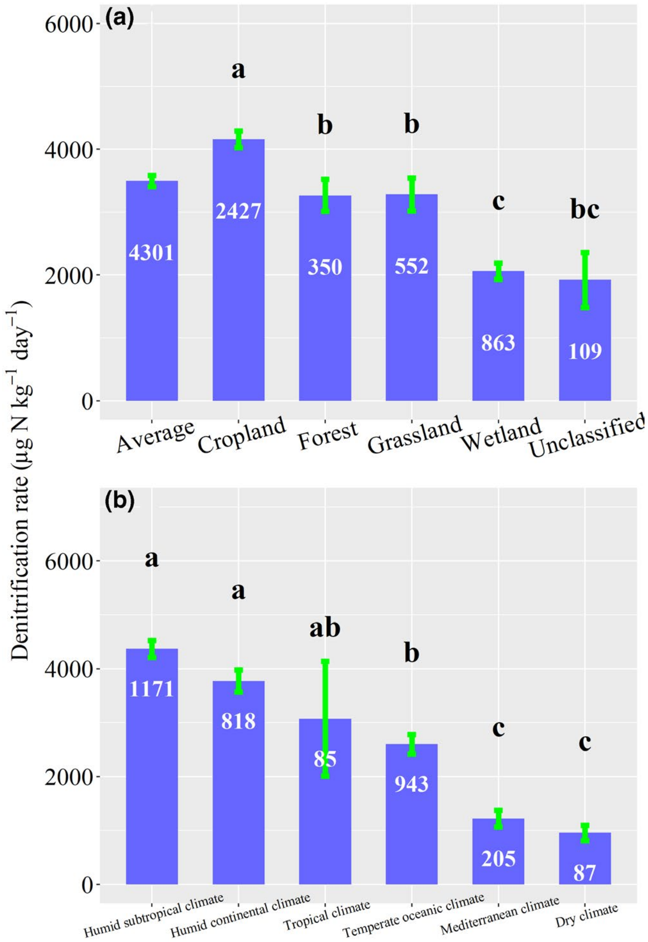

FIGURE 1 Differences in the denitrification rate with ecosystems (a) and climate zones (b). The bars are standard error and the values are the numbers of observations in each ecosystem. The classification of climate zones was conducted based on Köppen Climate Classification. Humid subtropical climate includes monsoon-influenced humid subtropical climate. Humid continental climate includes Hot-summer humid continental climate and warm-summer humid continental climate. Tropical climate includes Tropical monsoon climate, Tropical rainforest climate, and Tropical wet-dry climate. Temperate oceanic climate includes Monsoon-influenced temperate oceanic climate. Mediterranean climate includes Hot-summer Mediterranean climate and Warm-summer Mediterranean climate. The average denitrification rate was presented with the observations being more than 80 (b). The different letters above bars indicate significantly differences in denitrification rate

Among the climate types, the denitrification rates were 4242.29 ± 152.32 μg N kg^{-1} soil day^{-1} (Num = 1171, Figure 1b) under humid subtropical climates, 3904.60 ± 210.46 μg N kg^{-1} soil day^{-1} (Num = 818) under humid continental climates, and 2896.96 ± 958.26 μg N kg^{-1} soil day^{-1} (Num = 85) under tropical climates. There were no significant differences in denitrification rate across the three aforementioned climate zones. The Mediterranean climates (1384.61 ± 181.42 μg N kg^{-1} soil day^{-1}, Num = 205) and dry climates (965.80 ± 150.35 μg N kg^{-1} soil day^{-1}, Num = 87) had the lowest denitrification rate among climatic zones. Additionally, soil denitrification rate decreased with latitude, with the slope being −0.03 ($p = .06$) in the northern hemisphere and −0.09 ($p = .05$) in the southern hemisphere (Figure S2).

3.2 | The changes of denitrification rate with environmental variables

Denitrification rate significantly increased with MAT (p = .04, Num = 3559) and MAP (p = .006, Num = 3596) at a global scale (Figure 2).

Regarding soil properties, denitrification rate significantly decreased with soil clay contents at a global scale ($p < .001$, Num = 1956)

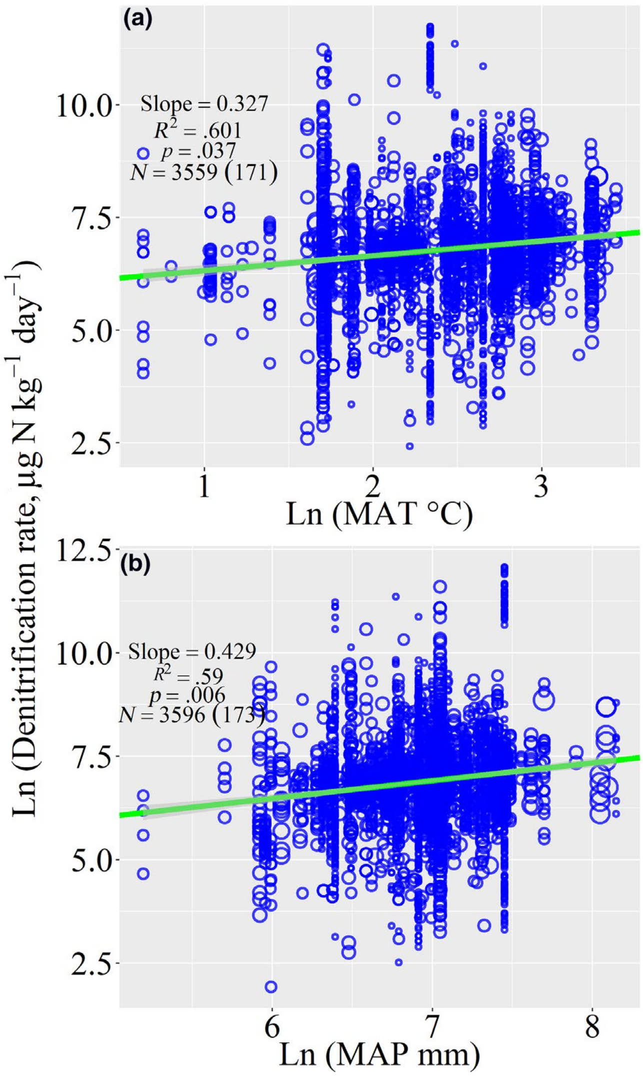

FIGURE 2 The bivariate relationships of denitrification rate with climatic factors, mean annual temperature (MAT, a) and mean annual precipitation (MAP, b) using the logarithmically transformed data at a global scale. The green lines are the slopes ±95% confidence intervals with grey color from the linear mixed effects models. The size of circles is the number of replicates in each study from 1 to 48. The number before parentheses is the observations and the number in parentheses is for studies

(Figure 3) but did not demonstrate a significant relationship with soil sand content ($p = .20$, Num = 1677; Figure S3). Soil denitrification rate tended to decrease with soil bulk density ($p = .42$; Num = 836, Figure S4). Furthermore, the denitrification rate significantly increased with soil pH ($p = .002$, Num = 3521), SM ($p < .001$, Num = 1043, Figure 3), and water-filled pore space ($p < .001$; Num = 728, Figure S5). The denitrification rate increased with the contents of soil organic carbon (SOC) ($p < .001$, Num = 3318), dissolved organic carbon ($p < .001$, Num = 613), total soil N ($p < .001$, Num = 2640), dissolved organic N ($p < .001$, Num = 116), ammonium ($p < .001$, Num = 1978), and nitrate ($p < .001$, Num = 2493, Figure 3). However, there was no significant relationship between denitrification rate and soil C:N ratio at a global scale ($p = .56$, Num = 2368; Figure S6).

Denitrification rate was regulated by soil microbial traits (Figure 4). To be specific, the denitrification rate significantly increased with soil MBC ($p < .001$, Num = 550) and MBN ($p < .001$, Num = 282) at a global scale. No significant relationship was observed between denitrification rate and the ratio of MBC:MBN ($p = .52$, Num = 126) in this study.

3.3 | The multivariable relationships between denitrification rate and environmental factors

The results of structural equation models revealed that the direct effects of soil N contents, soil properties, and climate on global denitrification rate (Figure 5). Soil N contents played an important role in denitrification rate. Soil nitrate content significantly promoted denitrification rate with the standard coefficient of 0.14 ($p < .001$). Soil ammonium and total soil N also showed significantly positive effects on the denitrification rate with standard coefficient of 0.11 and 0.10 (both $p < .001$), respectively. Higher MAT (standard coefficient = 0.12, $p < .001$), soil pH (standard coefficients = 0.05, $p = .002$) and SM (standard coefficients = .04, $p = .003$) could favor soil denitrification, whereas higher soil clay content hampered denitrification (standard coefficient = −0.08, $p < .001$). Collectively, the direct effect of soil N substrates (joint coefficient = 0.35) was obviously greater than the effects of other soil properties and climate (joint coefficient = 0.13) in structural equation models.

Soil microbial biomass was also an important factor for denitrification rate. Because soil microbial biomass had a direct effect on denitrification in structural equation models and greater microbial biomass significantly promoted denitrification rate with standard coefficient of 0.10 ($p < .001$). Additionally, soil properties could indirectly influence denitrification rate by changing soil microbial biomass since soil nitrate (standard coefficient = 0.04, $p = .01$), ammonium (standard coefficient = 0.07, $p < .001$), and total soil N (standard coefficient = 0.10, $p < .001$) could increase soil microbial biomass and subsequently stimulate the denitrification rate in structural equation models.

Together, soil N substrates, MAT, soil pH, SM, and clay content accounted for 60% of the variations in denitrification rate at a global scale.

3.4 | The bivariate relationships between denitrification rate and environmental variables in different ecosystem types

The denitrification rate showed similar relationships with environmental variables across croplands, forests, grasslands, and wetlands (Figure 6). First, the denitrification rate was significantly and positively related to soil N contents in each ecosystem type. For instance, denitrification rate was positively correlated with soil nitrate contents (weighted slope = 0.14, $p < .001$ in croplands; slope = 0.20, $p < .001$ in forests; slope = 0.16, $p = .003$ in grasslands; slope = 0.26, $p < .001$ in wetlands) and total soil N (weighted slope = 0.14, $p < .001$ in croplands; slope = 0.20, $p < .001$ in forests; slope = 0.19, $p = .003$ in grasslands; slope = 0.36, $p < .001$ in wetlands). The denitrification rate was also positively related to soil ammonium in croplands (weighted slope = 0.21, $p < .001$), forests (weighted slope = 0.31, $p < .001$), and wetlands (weighted slope = 0.22, $p < .001$). Second, denitrification rate was generally and positively correlated with soil microbial biomass. The significant relations between denitrification rate and MBC were consistent in croplands (weighted slope = 0.30, $p < .001$), forests (weighted slope = 0.38, $p < .001$), grasslands (weighted slope = 0.42, $p < .001$), and wetlands (weighted slope = 0.18, $p < .001$).

4 | DISCUSSION

This study revealed the general patterns and controlling factors of denitrification rate in terrestrial ecosystems. Soil N contents (nitrate, ammonium, and organic N) accounted for the most variation in denitrification rate. Soil microbial biomass was also an important driver of denitrification at a global scale. Current denitrification models have not considered these factors comprehensively. The findings in this study are helpful in promoting the parameterization of denitrification modules in models.

4.1 | The main controlling factors of denitrification at a global scale

Although soil physical and chemical properties regulated the rate of denitrification, soil nitrate, ammonium, and total N explained most of the variation in denitrification rates at a global scale. Soil nitrate, the reactant of conventional denitrification, explained 24.1% of variation in global denitrification rate. In general, the changes in denitrification rate with soil nitrate contents are best described by a Michaelis–Menten function in which the denitrification rate rises with greater soil nitrate contents (Strong & Fillery, 2002). This relationship occurs because greater soil nitrate contents increase soil denitrifier abundance (coefficient from 0.232 to 0.361) (Xiong et al., 2017) and denitrifier activity (e.g., the nirS-type denitrifier) to exude nitrite reductase (Enwall et al., 2010). Furthermore, the enzymatic activity of denitrification can increase with the greater nitrate

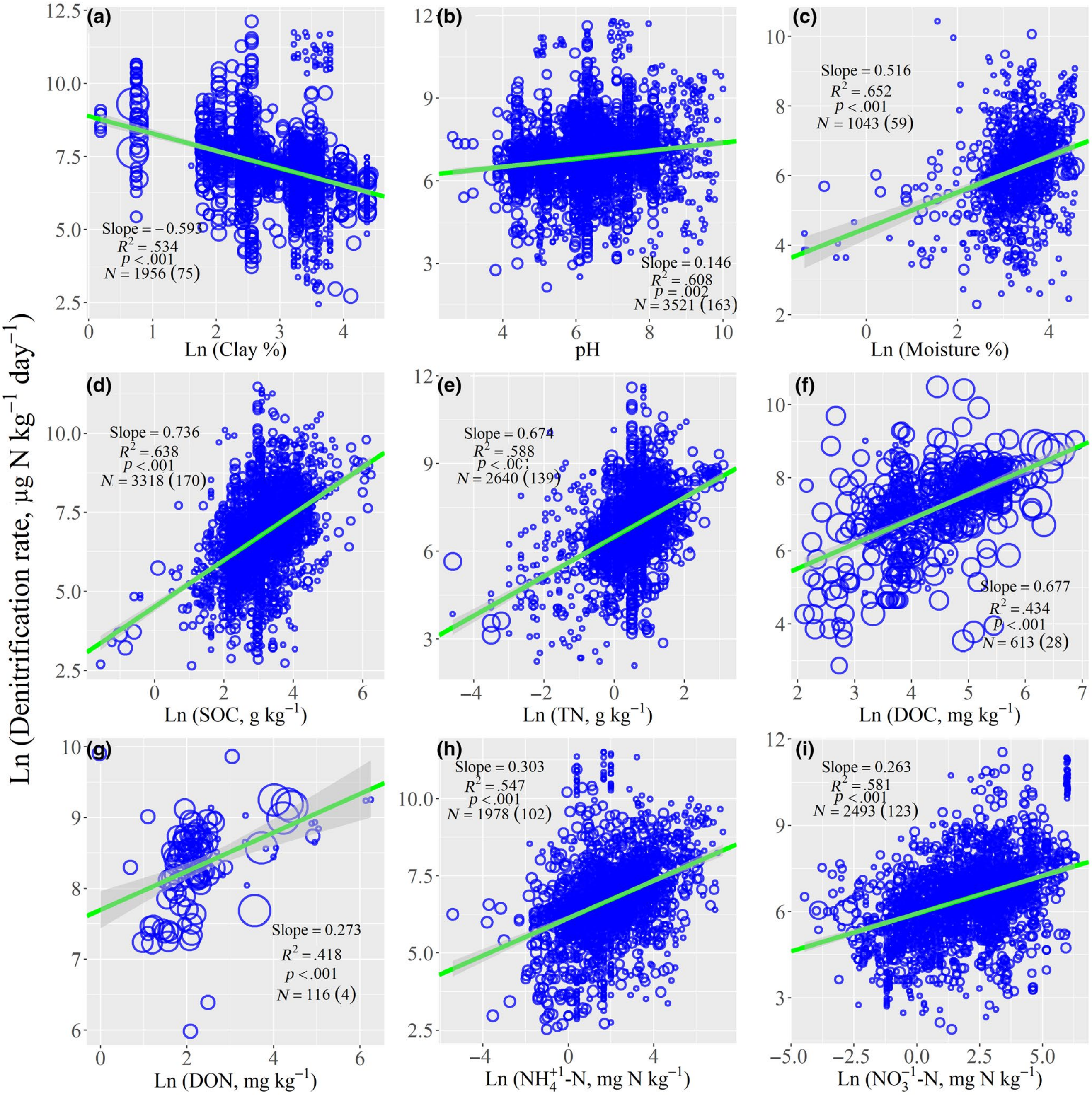

FIGURE 3 The bivariate relationships of denitrification rate against soil properties: soil clay content (a), pH (b), soil moisture (c), soil organic carbon (SOC, d), total soil N (TN, e), soil dissolved organic carbon (DOC, f), soil dissolved organic N (DON, g), soil ammonium (NH_4^+–N, h), and soil nitrate (NO_3^-–N, i) using the logarithmically transformed data. The green lines with grey shadings are the slopes ±95% confidence intervals. The size of circles is the number of replicates in each study from 1 to 48. The number before parentheses is the observations and the number in parentheses is for studies

content, which consequently promotes denitrification rate (White & Reddy, 1999). Therefore, nitrate addition often strengthens the contribution of soil nitrate to denitrification rate (Xiong et al., 2017).

The changes in soil ammonium contents accounted for 19.5% of variation in denitrification rates at a global scale. Soil ammonium is the precursor of the substrate of soil nitrifier denitrification that have been identified by Ritchie and Nicholas (1972). In this process, ammonium is oxidized to nitrite and then nitrite is reduced to nitric oxide and eventually to molecular nitrogen (Wrage et al., 2001). Evidence suggests that some species of *Nitrospira* can oxidize ammonium all the way to nitrate (Daims et al., 2015), but the *Nitrosospira tenuis* and *Nitrosospira europaea* can participate into denitrification (Shaw et al., 2006). Furthermore, *Nitrosomonas europaea* can also denitrify nitrite as a terminal electron acceptor (Poth & Focht, 1985). Some archaea and fungi are reported to participate in denitrification (Vajrala et al., 2013; Wrage-Monnig et al., 2018). Wrage et al.

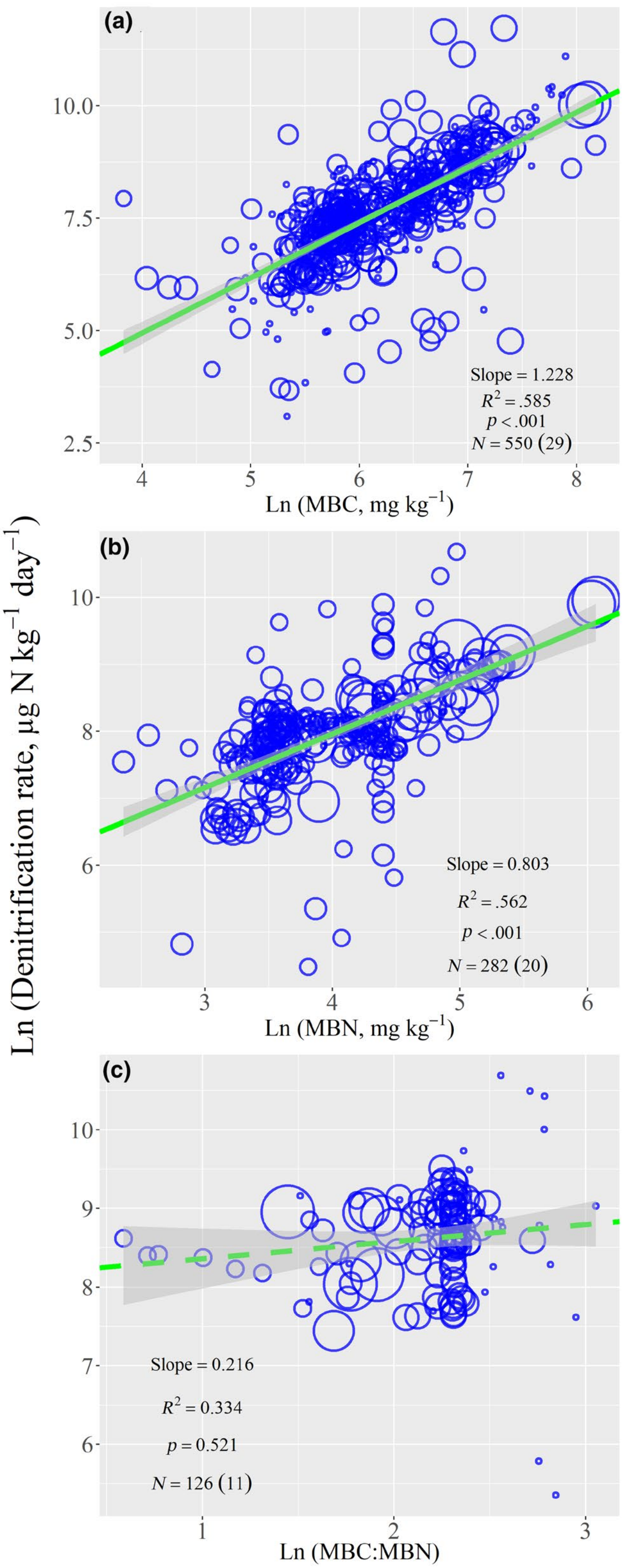

FIGURE 4 The bivariate relationships of denitrification rate against soil microbial characteristics: microbial biomass carbon (MBC, a), microbial biomass N (MBN, b), and the ratio of MBC:MBN (c) using the logarithmically transformed data. The green lines with grey shadings are the slopes ±95% confidence intervals. The size of circles is the number of replicates in each study from 1 to 48. The number before parentheses is the number of observations and the number in parentheses is for studies

(2004) reveals that nitrifier denitrification accounts for 8.3% of total denitrification on average; the percentage of nitrifier denitrification rises to 66.0%–77.5% when soil ammonium content is much higher than nitrate content. Thus, soil ammonium plays an important role in regulating total denitrification rate through nitrifier denitrification, and the contribution of nitrifier denitrification to total denitrification varies remarkably depending on environmental factors (e.g., SM, temperature, and soil oxic-anoxic conditions). Under suboptimal moisture conditions, soil nitrifier denitrification is the major pathway of total denitrification (Kool et al., 2011). In low temperature zones (below 10°C, e.g., arctic zone), nitrifier denitrification is likely to dominate total denitrification (Ma et al., 2007). Moreover, fluctuating oxic-anoxic conditions are apt for nitrifier denitrification (Chandran et al., 2011; Yu et al., 2018). Therefore, soil ammonium contents may be important for denitrification via nitrifier denitrification under lower temperature or transient oxic-anoxic conditions.

Soil total N content also substantially regulates total denitrification rates at a global scale (18.1%). Previous study found that soil denitrification rate increased by 164%–331%, whereas soil nitrate contents only increased by 34.2% (Malique et al., 2019). The massive increase in soil denitrification rate was speculated to come from the codenitrification process because the organic N content coincidentally increased by 321%. Codenitrification refers to that soil organic N reacts with nitrite to form nitrous oxide (Wrage-Monnig et al., 2018). A recent study showed that hydroxylamine, phenylalanine, and glycine are the substrates of codenitrification (Rex et al., 2019). Codenitrification was reported to contribute to 33% of soil N_2O production and 3% of N_2 production after urine addition (Rex et al., 2018). Additionally, soil organic N can be mineralized to ammonium (Li et al., 2019) to provide substrate for nitrifier denitrification, and soil organic N can be nitrified to nitrate through heterotrophic nitrification (Li et al., 2020) to provide substrates for conventional denitrification. Collectively, the important role of soil nitrate, ammonium, and total organic N on denitrification rate supported our H_1 that the joint effect of different soil N substrates in denitrification explained the majority of variance in global denitrification rates.

Soil microbes also play remarkable roles in the rate of denitrification. Many kinds of microbes participate into the denitrification process, such as bacteria, fungi (Rex et al., 2019; Senbayram et al., 2018), and archaea (Wrage-Monnig et al., 2018). Many types of soil bacteria can express denitrifying reductases, such as alphaproteobacteria, beta-proteobacteria, and gamma-proteobacteria (Philippot, 2002). Fungi also harbors nirK gene that can express nitrite reductase to take part in denitrification (Lourenco et al., 2018). Moreover, some archaea possess denitrifying genes, for example, *Pyrobaculum aerophilum* holds narG, nirS, and norZ (Philippot, 2002). Furthermore, soil N can indirectly influence the denitrification rate by changing soil microbes, in addition to its direct effect as the substrate (Figure 5). The N addition usually accelerates denitrification rate as a results of increasing soil microbial biomass (Yao et al., 2018). A recent study confirmed that higher rates of denitrification occur due to the higher abundance of denitrifier with increasing soil N substrate (Regan et al., 2017).

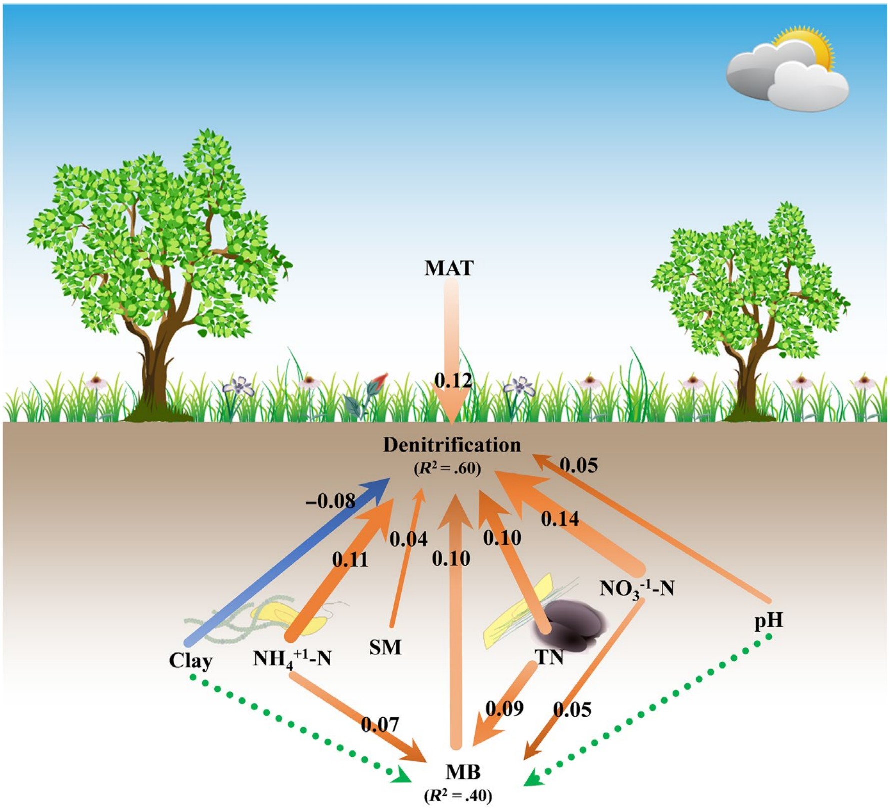

FIGURE 5 The multiple relationships of denitrification rate at the global scale. The orange lines stand for significantly positive relationships, blue lines stand for negative relationships, and the green dashed lines stand for insignificant relationships where the statistically significant level is set at $\alpha \le .05$. Numbers stand for standardized coefficients. MAT, SM, TN, and MBN are mean annual temperature, soil moisture, total soil N, and microbial biomass N, respectively

Therefore, soil microbes are an important cog in denitrification at the global scale (H_2).

MAT is a prominent climatic factor controlling denitrification at a global scale. As reported, the temperature sensitivity of denitrification rate was approximately 2 (Stanford et al., 1975), indicating denitrification rate increases with higher temperature. The positive relationship between denitrification rate and temperature may result from three reasons. First, higher temperature can stimulate soil denitrifier activity. Cui et al. (2016) reveal that nirS-type denitrifier abundance increases from approximately 9×10^6 to 1.5×10^7 copies when temperature rises from 15 to 35°C. Second, the higher temperature can increase N substrate contents for denitrification. Soil nitrate concentration increases by 96.3% and ammonium concentration increases by 352% when temperature rises by 20°C (Cui et al., 2016). Third, higher temperature can increase the affinity of soil substrate for microbial denitrification. The index of affinity of soil nitrate at 35°C is approximately two orders of magnitude greater than the affinity index at 20°C (Maggi & Riley, 2015).

SM is considered as an important factor to regulate denitrification in some experimental studies; however, its role is less important in determining the global variation in denitrification rate. Although denitrification rate increases with soil water content ranging from 18.4% to 37.5% in paddy soils (saturated volumetric water content was from 46.4 to 51.2 cm cm^{-3}), the significant increases in denitrification rate with more soil water generally occur at lower SMs, while the denitrification rate usually does not change when SM is greater than 30 cm cm^{-3} (Tan et al., 2018a). Most SM in our data set (approximately 60%) is greater than 25%. In addition, the denitrification rate is more likely to be changed under drying-wetting conditions rather than under relatively stable SM (Dong et al., 2012). The SM in our dataset only changed marginally, thus, we were unable to properly capture the effect of SM on global denitrification rate.

The influences of soil pH on denitrification is complex as there is no optimum pH for denitrification (Šimek et al., 2002). The positive relation between denitrification rate and pH is attributed to the role that higher pH can alleviate mineral nitrogen limitation to microbes (Šimek & Cooper, 2002). We also found that the concentrations of SOC significantly influenced denitrification rate, because the higher organic carbon content benefits the initiation of the denitrification (Saggar et al., 2013), and the addition of glucose and acetate increases denitrification rate (Shan et al., 2018).

4.2 | The implications for denitrification changes

Anthropogenic activities will significantly change denitrification by altering the soil N contents, microbial biomass, and temperature, which are the main controlling factors of denitrification rates at a global scale (Figure 5). Fertilization and N deposition could, on the one hand, significantly increase the total soil N; on the other hand, it may decrease soil microbial biomass under higher N inputs (Chen et al., 2015; Jian et al., 2016). For example, N addition significantly increases total soil N by 6.2% but decreases soil microbial biomass by 5.8% at a global scale (Lu et al., 2011), therefore, the effects of N addition on denitrification rate may be marginal due to the competing

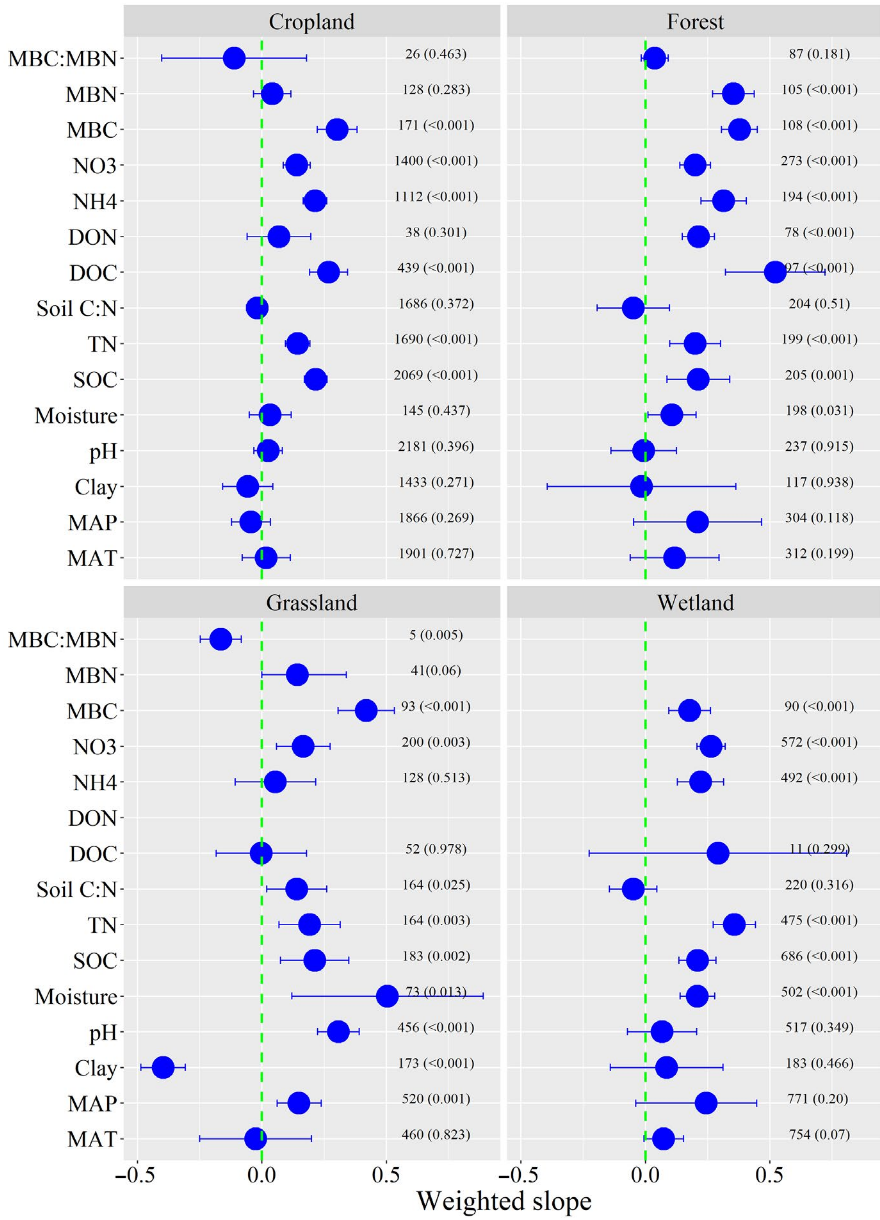

FIGURE 6 The slopes from bivariate relationships of denitrification rate against MAT (mean annual temperature), MAP (mean annual precipitation), Clay, pH, Moisture, soil organic carbon (SOC), total soil N (TN), soil C:N, DOC (soil dissolved organic carbon), dissolved organic N (DON), NH_4-N, NO_3-N, soil microbial biomass carbon (MBC), microbial biomass N (MBN), MBC:MBN in each terrestrial ecosystem. The blue dot is averaged slope, and the bars are 95% confidence intervals. The values are the number of observations outside parentheses and the *p* values inside parentheses

effects between substrates and microbial biomass. However, given that soil nitrate increased by 428.6% under N inputs (Lu et al., 2011), the effects of increasing soil N substrate may overwhelm the reduction in microbial biomass on denitrification, thereby eventually increasing soil denitrification rate. A recent study confirmed that denitrification substantially increases (by 174%) under greater N substrates despite a reduction in soil microbial biomass (Wang et al., 2018). The usage of N fertilizer and manure continuously rises in order to meet the food requirement for a growing human population around the world (Tian et al., 2018), and the denitrification rate is expected to rise correspondingly in the near future.

Global warming will stimulate denitrification rate directly and also indirectly by increasing soil N substrate and microbial biomass. Soil inorganic N has increased by 17.9% under warming (Bai et al., 2013), which may result from the higher soil N mineralization (Bai et al., 2013) and nitrification (Li et al., 2020) under higher temperatures. A meta-analysis revealed that the average of soil microbial biomass increases by approximately 3.6% under global warming (Xu & Yuan, 2017). The higher soil inorganic N and microbial biomass will promote soil denitrification. Moreover, the increase in soil microbial biomass was greater in areas of high altitude or latitude. In a study on Tibetan plateau, Zhang et al. (2015) find soil microbial biomass has increased by 14.3%, suggesting that warming may increase denitrification rate to a greater extent in higher altitude and latitude.

These findings are helpful to develop models for simulating denitrification. First, the data set of denitrification rate that compiled 4301 observations across main terrestrial ecosystems offers a benchmark for denitrification models. Second, there are many models to simulate denitrification, such as CLM-CN, DLEM, LM3Y-N, LPJ-GUESS, LPX-Bern, O-CN, ORCHIDEE, ORCHIDEE-CNP, TRIPLEX-GHG, and VISIT. However, these models typically focus on soil nitrate contents and general physical and chemical properties of the soil (Tian et al., 2018), whereas these models have rarely considered the role of soil organic N and soil microbes. Additionally, among these models, only LM3V-N take soil ammonium contents into account (Tian et al., 2018). The remarkable effects of soil ammonium, soil organic N, and microbial biomass on denitrification rate revealed in this study indicate that future models should also take into consideration these factors.

4.3 | Limitation

There are some limitations in this global synthesis on denitrification. First, SM usually influences soil redox condition/O_2 concentrations that are critical for the denitrification (Osaka et al., 2018). Although we tested the effects of SM on denitrification rate in this study, we did not explore the effect of soil redox condition because of data paucity. Second, many types of soil microbes can participate in denitrification, and some studies found the changes of soil microbial community also influence the denitrification rate (e.g., Philippot et al., 2013). Additionally, functional microbes may affect denitrification (Levy-Booth et al., 2014). We were unable to test the effects of microbial community or functional microbes on denitrification rate due to a lack of global-level data. Third, we found soil nitrate, ammonium, and organic N play important roles in determining denitrification rate at a global scale, implying that they may influence total denitrification via different pathways. This avenue remains to be further tested using an isotopic approach at large spatial scales. Fourth, although the acetylene inhibition method is the most commonly used method to measure denitrification rate, the denitrification rate may be underestimated because acetylene could inhibit the production of nitrate via nitrification (Groffman et al., 2006; Watts & Seitzinger, 2000).

This study is among the first attempts to comprehensively analyze the patterns and controlling factors of denitrification rate in terrestrial ecosystems. Denitrification rate varied with ecosystems/climate zones and was mainly determined by soil N contents (nitrate, ammonium, and total soil N) at a global scale. We also found that soil microbes play an important role in regulating denitrification rate, in which the significant changes in soil microbial biomass under anthropogenic activities and/or climate change could eventually influence denitrification rate. This work highlights the importance of incorporating different soil N contents and microbial biomass into models to accurately project denitrification and N cycling.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

Li Z designed the research, collected data, and performed the analyses. Li Z and Niu S wrote the first draft. All the authors contributed to the writing of the paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in https://doi.org/10.5061/dryad.c866t1g87.

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REFERENCES

Almaraz, M., Wong, M., & Yang, W. (2020). Looking back to look ahead: A vision for soil denitrification research. *Ecology*, *101*, e02917. https://doi.org/10.1002/ecy.2917

Attard, E., Recous, S., Chabbi, A., De Berranger, C., Guillaumaud, N., Labreuche, J., Philippot, L., Schmid, B., & Le Roux, X. (2011). Soil environmental conditions rather than denitrifier abundance and diversity drive potential denitrification after changes in land uses. *Global Change Biology*, *17*(5), 1975–1989. https://doi.org/10.1111/j.1365-2486.2010.02340.x

Bai, E., Li, S., Xu, W., Li, W., Dai, W., & Jiang, P. (2013). A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist*, *199*, 441–451. https://doi.org/10.1111/nph.12252

Barnard, R., Le Roux, X., Hungate, B. A., Cleland, E. E., Blankinship, J. C., Barthes, L., & Leadley, P. W. (2006). Several components of global change alter nitrifying and denitrifying activities in an annual grassland. *Functional Ecology*, *20*(4), 557–564. https://doi.org/10.1111/j.1365-2435.2006.01146.x

Bonnett, S., Blackwell, M., Leah, R., Cook, V., O'Connor, M., & Maltby, E. (2013). Temperature response of denitrification rate and greenhouse gas production in agricultural river marginal wetland soils. *Geobiology*, *11*, 252–267. https://doi.org/10.1111/gbi.12032

Bouwman, A. F., Beusen, A. H., Griffioen, J., Van Groenigen, J. W., Hefting, M. M., Oenema, O., Van Puijenbroek, P. J. T. M., Seitzinger, S., Slomp, C. P., & Stehfest, E. (2013). Global trends and uncertainties in terrestrial denitrification and N_2O emissions. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *368*(1621), 20130112.

Chandran, K., Stein, L. Y, Klotz, M. G., & van Loosdrecht, M. C. M. (2011). Nitrous oxide production by lithotrophic ammonia-oxidizing bacteria and implications for engineered nitrogen removal systems. *Biochemical Society Transactions*, *39*(6), 1832–1837. https://doi.org/10.1042/BST20110717

Chen, H., Li, D., Gurmesa, G., Yu, G., Li, L., Zhang, W., Fang, H., & Mo, J. (2015). Effects of nitrogen deposition on carbon cycle in terrestrial ecosystems of China: A meta-analysis. *Environmental Pollution*, *206*, 352–360. https://doi.org/10.1016/j.envpol.2015.07.033

Cuhel, J., & Simek, M. (2011). Proximal and distal control by pH of denitrification rate in a pasture soil. *Agriculture Ecosystems & Environment*, *141*, 230–233. https://doi.org/10.1016/j.agee.2011.02.016

Cui, P., Fan, F., Yin, C., Song, A., Huang, P., Tang, Y., Zhu, P., Peng, C., Li, T., Wakelin, S., & Liang, Y. (2016). Long-term organic and inorganic fertilization alters temperature sensitivity of potential N_2O emissions and associated microbes. *Soil Biology & Biochemistry*, *93*, 131–141. https://doi.org/10.1016/j.soilbio.2015.11.005

Cui, S., Shi, Y., Groffman, P., Schlesinger, W., & Zhu, Y. (2013). Centennial-scale analysis of the creation and fate of reactive nitrogen in China (1910–2010). *Proceedings of the National Academy of Sciences of the United States of America*, *110*(6), 2052–2057. https://doi.org/10.1073/pnas.1221638110

Daims, H., Lebedeva, E., Pjevac, P., Han, P., Herbold, C., Albertsen, M., Jehmlich, N., Palatinszky, M., Vierheilig, J., Bulaev, A., Kirkegaard, R., von Bergen, M., Rattei, T., Bendinger, B., Nielsen, P., & Wagner, M. (2015). Complete nitrification by *Nitrospira* bacteria. *Nature*, *528*, 504–509. https://doi.org/10.1038/nature16461

Dong, N., Brandt, K., Sorensen, J., Hung, N., Hach, C., Tan, P., & Dalsgaard, T. (2012). Effects of alternating wetting and drying versus continuous flooding on fertilizer nitrogen fate in rice fields in the Mekong Delta, Vietnam. *Soil Biology & Biochemistry*, *47*, 166–174. https://doi.org/10.1016/j.soilbio.2011.12.028

Duan, P., Song, Y., Li, S., & Xiong, Z. (2019). Responses of N_2O production pathways and related functional microbes to temperature across greenhouse vegetable field soils. *Geoderma*, *355*, 113904. https://doi.org/10.1016/j.geoderma.2019.113904

Enwall, K., Throback, I., Stenberg, M., Soderstrom, M., & Hallin, S. (2010). Soil resources influence spatial patterns of denitrifying communities at scales compatible with land management. *Applied and Environmental Microbiology*, *76*(7), 2243–2250. https://doi.org/10.1128/AEM.02197-09

Groffman, P. M. (2012). Terrestrial denitrification: Challenges and opportunities. *Ecological Processes*, *1*, 1–11. https://doi.org/10.1186/2192-1709-1-11

Groffman, P. M., Altabet, M. A., Böhlke, J. K., Butterbach-Bahl, K., David, M. B., Firestone, M. K., Giblin, A. E., Kana, T. M., Nielsen, L. P., & Voytek, M. A. (2006). Methods for measuring denitrification: diverse approaches to a difficult problem. *Ecological Applications*, *16*, 2091–2122. https://doi.org/10.1890/1051-0761(2006)016[2091:MFMDDA]2.0.CO;2

Groffman, P., & Tiedje, J. (1988). Denitrification hysteresis during wetting and drying cycles in soil. *Soil Science Society of America Journal*, *52*, 1626–1629. https://doi.org/10.2136/sssaj1988.03615995005200060022x

Hall, J., Paterson, E., & Killham, K. (1998). The effect of elevated CO_2 concentration and soil pH on the relationship between plant growth and rhizosphere denitrification potential. *Global Change Biology*, *4*(2), 209–216. https://doi.org/10.1046/j.1365-2486.1998.00124.x

Hayatsu, M., Tago, K., & Saito, M. (2008). Various players in the nitrogen cycle: Diversity and functions of the microorganisms involved in nitrification and denitrification. *Soil Science and Plant Nutrition*, *54*, 33–45. https://doi.org/10.1111/j.1747-0765.2007.00195.x

Holtan-Hartwig, L., Dörsch, P., & Bakken, L. R. (2000). Comparison of denitrifying communities in organic soils: kinetics of NO_3^- and N_2O reduction. *Soil Biology & Biochemistry*, *32*, 833–843. https://doi.org/10.1016/S0038-0717(99)00213-8

Holtan-Hartwig, L., Dörsch, P., & Bakken, L. (2002). Low temperature control of soil denitrifying communities: kinetics of N_2O production and reduction. *Soil Biology & Biochemistry*, *34*, 1797–1806. https://doi.org/10.1016/S0038-0717(02)00169-4

Hu, Z., Ling, H., Chen, S., Shen, S., Zhang, H., & Sun, Y. (2013). Soil respiration, nitrification, and denitrification in a wheat farmland soil under different managements. *Communications in Soil Science and Plant Analysis*, *44*, 3092–3102. https://doi.org/10.1080/00103624.2013.832290

Jian, S., Li, J., Chen, J., Wang, G., Mayes, M., Dzantor, K., Hui, D., & Luo, Y. (2016). Soil extracellular enzyme activities, soil carbon and nitrogen storage under nitrogen fertilization: A meta-analysis. *Soil Biology & Biochemistry*, *101*, 32–43. https://doi.org/10.1016/j.soilbio.2016.07.003

Jones, C. M., Graf, D. R. H., Bru, D., Philippot, L., & Hallin, S. (2013). The unaccounted yet abundant nitrous oxide-reducing microbial community: a potential nitrous oxide sink. *The ISME Journal*, *7*, 417–426. https://doi.org/10.1038/ismej.2012.125

Jones, L. C., Peters, B., Pacheco, J. S. L., Casciotti, K. L., & Fendorf, S. (2015). Stable isotopes and iron oxide mineral products as markers of chemodenitrification. *Environmental Science & Technology*, *49*, 3444–3452. https://doi.org/10.1021/es504862x

Kool, D., Dolfing, J., Wrage, N., & Van Groenigen, J. (2011). Nitrifier denitrification as a distinct and significant source of nitrous oxide from soil. *Soil Biology & Biochemistry*, *43*, 174–178. https://doi.org/10.1016/j.soilbio.2010.09.030

Kuypers, M., Marchant, H., & Kartal, B. (2018). The microbial nitrogen-cycling network. *Nature Reviews Microbiology*, *16*, 263–276. https://doi.org/10.1038/nrmicro.2018.9

Levy-Booth, D., Prescott, C., & Grayston, S. (2014). Microbial functional genes involved in nitrogen fixation, nitrification and denitrification in forest ecosystems. *Soil Biology & Biochemistry*, *75*, 11–25. https://doi.org/10.1016/j.soilbio.2014.03.021

Li, X., McCarty, G., Lang, M., Ducey, T., Hunt, P., & Miller, J. (2018). Topographic and physicochemical controls on soil denitrification in prior converted croplands located on the Delmarva Peninsula, USA. *Geoderma*, *309*, 41–49. https://doi.org/10.1016/j.geoderma.2017.09.003

Li, Z. (2021). Soil denitrification rate. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.c866t1g87

Li, Z., Tian, D., Wang, B., Wang, J., Wang, S., Chen, H. Y. H., Xu, X., Wang, C., He, N., & Niu, S. (2019). Microbes drive global soil nitrogen mineralization and availability. *Global Change Biology*, *25*, 1078–1088. https://doi.org/10.1111/gcb.14557

Li, Z., Zeng, Z., Tian, D., Wang, J., Fu, Z., Zhang, F., Zhang, R., Chen, W., Luo, Y., & Niu, S. (2020). Global patterns and controlling factors of soil nitrification rate. *Global Change Biology*, *26*, 4147–4157. https://doi.org/10.1111/gcb.15119

Lourenço, K. S., Dimitrov, M. R., Pijl, A., Soares, J. R., do Carmo, J. B., van Veen, J. A., Cantarella, H., & Kuramae, E. E. (2018). Dominance of bacterial ammonium oxidizers and fungal denitrifiers in the complex nitrogen cycle pathways related to nitrous oxide emission. *Global Change Biology Bioenergy*, *10*, 645–660. https://doi.org/10.1111/gcbb.12519

Lu, M., Yang, Y., Luo, Y., Fang, C., Zhou, X., Chen, J., Yang, X., & Li, B. (2011). Responses of ecosystem nitrogen cycle to nitrogen addition: A meta-analysis. *New Phytologist*, *189*(4), 1040–1050. https://doi.org/10.1111/j.1469-8137.2010.03563.x

Ma, W., Schautz, A., Fishback, L., Bedard-Haughn, A., Farrell, R., & Siciliano, S. (2007). Assessing the potential of ammonia oxidizing bacteria to produce nitrous oxide in soils of a high arctic lowland ecosystem on Devon Island, Canada. *Soil Biology & Biochemistry*, *39*, 2001–2013. https://doi.org/10.1016/j.soilbio.2007.03.001

Maggi, F., & Riley, W. (2015). The effect of temperature on the rate, affinity, and N-15 fractionation of NO_3^- during biological denitrification in soils. *Biogeochemistry*, *124*, 235–253.

Malique, F., Ke, P., Boettcher, J., Dannenmann, M., & Butterbach-Bahl, K. (2019). Plant and soil effects on denitrification potential in agricultural soils. *Plant and Soil*, *439*, 459–474. https://doi.org/10.1007/s11104-019-04038-5

Martinez-Espinosa, C., Sauvage, S., Al Bitar, A., Green, P., Vorosmarty, C., & Sanchez-Perez, J. (2021). Denitrification in wetlands: A review towards a quantification at global scale. *Science of the Total Environment*, *754*, 142398. https://doi.org/10.1016/j.scitotenv.2020.142398

Mohsenipour, M., Shahid, S., & Ebrahimi, K. (2015). Nitrate adsorption on clay kaolin: Batch tests. *Journal of Chemistry*, *2015*, 397069. https://doi.org/10.1155/2015/397069

Osaka, K., Nakajima, Y., Suzuki, K., Eguchi, S., & Katou, H. (2018). Nitrogen and oxygen isotope enrichment factors of nitrate at different denitrification rates in an agricultural soil. *Soil Science* and Plant Nutrition, 64, 558–565. https://doi.org/10.1080/00380768.2018.1504321

Pan, F., Chapman, S., Li, Y., & Yao, H. (2017). Straw amendment to paddy soil stimulates denitrification but biochar amendment promotes anaerobic ammonia oxidation. *Journal of Soils and Sediments*, *17*, 2428–2437. https://doi.org/10.1007/s11368-017-1694-4

Philippot, L. (2002). Denitrifying genes in bacterial and archaeal genomes. *Biochimica Et Biophysica Acta-Gene Structure and Expression*, *1577*(3), 355–376. https://doi.org/10.1016/S0167-4781(02)00420-7

Philippot, L., Spor, A., Henault, C., Bru, D., Bizouard, F., Jones, C., Sarr, A., & Maron, P. (2013). Loss in microbial diversity affects nitrogen cycling in soil. *The ISME Journal*, *7*, 1609–1619. https://doi.org/10.1038/ismej.2013.34

Poth, M., & Focht, D. (1985). N-15 kinetic analysis of N_2O production by *nitrosomonas europaea*- an examination of nitrifier denitrification. *Applied and Environmental Microbiology*, *49*(5), 1134–1141.

Regan, K., Stempfhuber, B., Schloter, M., Rasche, F., Prati, D., Philippot, L., Boeddinghaus, R., Kandeler, E., & Marhan, S. (2017). Spatial and temporal dynamics of nitrogen fixing, nitrifying and denitrifying microbes in an unfertilized grassland soil. *Soil Biology & Biochemistry*, *109*, 214–226. https://doi.org/10.1016/j.soilbio.2016.11.011

Rex, D., Clough, T., Richards, K., Condron, L., de Klein, C., Morales, S., & Lanigan, G. (2019). Impact of nitrogen compounds on fungal and bacterial contributions to codenitrification in a pasture soil. *Scientific Reports*, *9*, 13371. https://doi.org/10.1038/s41598-019-49989-y

Rex, D., Clough, T. J., Richards, K. G., de Klein, C., Morales, S. E., Samad, M. S., Grant, J., & Lanigan, G. J. (2018). Fungal and bacterial contributions to codenitrification emissions of N_2O and N_2 following urea deposition to soil. *Nutrient Cycling in Agroecosystems*, *110*, 135–149. https://doi.org/10.1007/s10705-017-9901-7

Ritchie, G., & Nicholas, D. (1972). Identification of the sources of nitrous oxide produced by oxidative and reductive processes in *Nitrosomonas europaea*. *Biochemical Journal*, *126*, 1181–1191.

Saggar, S., Jha, N., Deslippe, J., Bolan, N., Luo, J., Giltrap, D., Kim, D.-G., Zaman, M., & Tillman, R. (2013). Denitrification and $N_2O:N_2$ production in temperate grasslands: Processes, measurements, modelling and mitigating negative impacts. *Science of the Total Environment*, *465*, 173–195. https://doi.org/10.1016/j.scitotenv.2012.11.050

Senbayram, M., Well, R., Bol, R., Chadwick, D., Jones, D., & Wu, D. (2018). Interaction of straw amendment and soil NO_3^- content controls fungal denitrification and denitrification product stoichiometry in a sandy soil. *Soil Biology & Biochemistry*, *126*, 204–212. https://doi.org/10.1016/j.soilbio.2018.09.005

Seo, D., & DeLaune, R. (2010). Fungal and bacterial mediated denitrification in wetlands: Influence of sediment redox condition. *Water Research*, *44*, 2441–2450. https://doi.org/10.1016/j.watres.2010.01.006

Shan, J., Yang, P., Shang, X., Rahman, M., & Yan, X. (2018). Anaerobic ammonium oxidation and denitrification in a paddy soil as affected by temperature, pH, organic carbon, and substrates. *Biology and Fertility of Soils*, *54*, 341–348. https://doi.org/10.1007/s00374-018-1263-z

Shaw, L., Nicol, G., Smith, Z., Fear, J., Prosser, J., & Baggs, E. (2006). *Nitrosospira spp*. can produce nitrous oxide via a nitrifier denitrification pathway. *Environmental Microbiology*, *8*, 214–222.

Silvennoinen, H., Liikanen, A., Torssonen, J., Stange, C., & Martikainen, P. (2008). Denitrification and N_2O effluxes in the Bothnian Bay (northern Baltic Sea) river sediments as affected by temperature under different oxygen concentrations. *Biogeochemistry*, *88*, 63–72. https://doi.org/10.1007/s10533-008-9194-7

Šimek, M., & Cooper, J. (2002). The influence of soil pH on denitrification: progress towards the understanding of this interaction over the last 50 years. *European Journal of Soil Science*, *53*(3), 345–354. https://doi.org/10.1046/j.1365-2389.2002.00461.x

Šimek, M., Jíšová, L., & Hopkins, D. W. (2002). What is the so-called optimum pH for denitrification in soil? *Soil Biology & Biochemistry*, *34*, 1227–1234. https://doi.org/10.1016/S0038-0717(02)00059-7

Stanford, G., Dzienia, S., & Vanderpol, R. (1975). Effect of temperature on denitrification rate in soils. *Soil Science Society of America Journal*, *39*(5), 867–870. https://doi.org/10.2136/sssaj1975.03615995003900050024x

Strong, D., & Fillery, I. (2002). Denitrification response to nitrate concentrations in sandy soils. *Soil Biology & Biochemistry*, *34*, 945–954. https://doi.org/10.1016/S0038-0717(02)00026-3

Tan, X., Shao, D., & Gu, W. (2018a). Effects of temperature and soil moisture on gross nitrification and denitrification rates of a Chinese lowland paddy field soil. *Paddy and Water Environment*, *16*, 687–698. https://doi.org/10.1007/s10333-018-0660-0

Tan, X. Z., Shao, D. G., & Gu, W. Q. (2018b). Effects of temperature and soil moisture on gross nitrification and denitrification rates of a Chinese lowland paddy field soil. *Paddy and Water Environment*, *16*, 687–698. https://doi.org/10.1007/s10333-018-0660-0

Tian, H., Yang, J., Lu, C., Xu, R., Canadell, J., Jackson, R., Arneth, A., Chang, J., Chen, G., Ciais, P., Gerber, S., Ito, A., Huang, Y., Joos, F., Lienert, S., Messina, P., Olin, S., Pan, S., Peng, C., … Zhu, Q. (2018). The global N_2O model intercomparison project. *Bulletin of the American Meteorological Society*, *99*, 1231–1252. https://doi.org/10.1175/BAMS-D-17-0212.1

Vajrala, N., Martens-Habbena, W., Sayavedra-Soto, L., Schauer, A., Bottomley, P., Stahl, D., & Arp, D. (2013). Hydroxylamine as an intermediate in ammonia oxidation by globally abundant marine archaea. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(3), 1006–1011. https://doi.org/10.1073/pnas.1214272110

Wallenstein, M., Myrold, D., Firestone, M., & Voytek, M. (2006). Environmental controls on denitrifying communities and denitrification rates: Insights from molecular methods. *Ecological Applications*, *16*, 2143–2152. https://doi.org/10.1890/1051-0761(2006)016[2143:ECODCA]2.0.CO;2

Wang, J., Chadwick, D., Cheng, Y., & Yan, X. (2018). Global analysis of agricultural soil denitrification in response to fertilizer nitrogen. *Science of the Total Environment*, *616*, 908–917. https://doi.org/10.1016/j.scitotenv.2017.10.229

Watts, S. H., & Seitzinger, S. P. (2000). Denitrification rates in organic and mineral soils from riparian sites: a comparison of N_2 flux and acetylene inhibition methods. *Soil Biology & Biochemistry*, *32*, 1383–1392. https://doi.org/10.1016/S0038-0717(00)00056-0

White, J., & Reddy, K. (1999). Influence of nitrate and phosphorus loading on denitrifying enzyme activity in Everglades wetland soils. *Soil Science Society of America Journal*, *63*, 1945–1954. https://doi.org/10.2136/sssaj1999.6361945x

Wrage, N., Velthof, G., Laanbroek, H., & Oenema, O. (2004). Nitrous oxide production in grassland soils: Assessing the contribution of nitrifier denitrification. *Soil Biology & Biochemistry*, *36*, 229–236. https://doi.org/10.1016/j.soilbio.2003.09.009

Wrage, N., Velthof, G., van Beusichem, M., & Oenema, O. (2001). Role of nitrifier denitrification in the production of nitrous oxide. *Soil Biology & Biochemistry*, *33*, 1723–1732. https://doi.org/10.1016/S0038-0717(01)00096-7

Wrage-Monnig, N., Horn, M., Well, R., Muller, C., Velthof, G., & Oenema, O. (2018). The role of nitrifier denitrification in the production of nitrous oxide revisited. *Soil Biology & Biochemistry*, *123*, A3–A16. https://doi.org/10.1016/j.soilbio.2018.03.020

Xiong, Z., Guo, L., Zhang, Q., Liu, G., & Liu, W. (2017). Edaphic conditions regulate denitrification directly and indirectly by altering denitrifier abundance in wetlands along the Han River, China. *Environmental Science & Technology*, *51*, 5483–5491. https://doi.org/10.1021/acs.est.6b06521

Xu, W., & Yuan, W. (2017). Responses of microbial biomass carbon and nitrogen to experimental warming: A meta-analysis. *Soil Biology & Biochemistry*, *115*, 265–274. https://doi.org/10.1016/j.soilbio.2017.08.033

Xu, Y., Xu, Z., Cai, Z., & Reverchon, F. (2013). Review of denitrification in tropical and subtropical soils of terrestrial ecosystems. *Journal of Soils and Sediments*, *13*, 699–710. https://doi.org/10.1007/s11368-013-0650-1

Yao, S., Groffman, P., Alewell, C., & Ballantine, K. (2018). Soil amendments promote denitrification in restored wetlands. *Restoration Ecology*, *26*, 294–302. https://doi.org/10.1111/rec.12573

Yu, R., Perez-Garcia, O., Lu, H., & Chandran, K. (2018). *Nitrosomonas europaea* adaptation to anoxic-oxic cycling: Insights from transcription analysis, proteomics and metabolic network modeling. *Science of the Total Environment*, *615*, 1566–1573. https://doi.org/10.1016/j.scitotenv.2017.09.142

Zhang, X., Shen, Z., & Fu, G. (2015). A meta-analysis of the effects of experimental warming on soil carbon and nitrogen dynamics on the Tibetan Plateau. *Applied Soil Ecology*, *87*, 32–38. https://doi.org/10.1016/j.apsoil.2014.11.012

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