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Elevated temperature shifts soil N cycling from microbial immobilization to enhanced mineralization, nitrification and denitrification across global terrestrial ecosystems

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Abstract

We assessed the response of soil microbial nitrogen (N) cycling and associated functional genes to elevated temperature at the global scale. A meta-analysis of 1,270 observations from 134 publications indicated that elevated temperature decreased soil microbial biomass N and increased N mineralization rates, both in the presence and absence of plants. These findings infer that elevated temperature drives microbially mediated N cycling processes from dominance by anabolic to catabolic reaction processes. Elevated temperature increased soil nitrification and denitrification rates, leading to an increase in N_2O emissions of up to 227%, whether plants were present or not. Rates of N mineralization, denitrification and N_2O emission demonstrated significant positive relationships with rates of CO_2 emissions under elevated temperatures, suggesting that microbial N cycling processes were associated with enhanced microbial carbon (C) metabolism due to soil warming. The response in the abundance of relevant genes to elevated temperature was not always consistent with changes in N cycling processes. While elevated temperature increased the abundances of the *nirS* gene with plants and *nosZ* genes without plants, there was no effect on the abundances of the ammonia-oxidizing archaea *amoA* gene, ammonia-oxidizing bacteria *amoA* and *nirK* genes. This study provides the first global-scale assessment demonstrating that elevated temperature shifts N cycling from microbial immobilization to enhanced mineralization, nitrification and denitrification in terrestrial ecosystems. These findings infer that elevated temperatures have a profound impact on global N cycling processes with implications of a positive feedback to global climate and emphasize the close linkage between soil microbial C and N cycling.

KEYWORDS

climate change, elevated temperature, functional genes, microbial carbon metabolism, nitrogen cycling, nitrous oxide, plant carbon

1 | INTRODUCTION

Global warming may lead to an increase of global surface temperature by up to 4.8°C during the 21st century based on various model projections, making it a serious concern to global sustainability and human sustenance (Cook et al., 2013; Dusenge, Duarte, & Way, 2018; Fernández-Martínez et al., 2019; IPCC, 2013; Richardson et al., 2018). Soil N pool size and fluxes, N availability to plants and N_2O emissions in terrestrial ecosystems are undoubtedly affected by microbially mediated N cycling such as N immobilization, mineralization, nitrification and denitrification, while these processes are also highly responsive to elevated temperatures. Various studies showed that elevated temperature alters microbial N immobilization and/or mineralization rates (Ma et al., 2011; Weedon et al., 2012; Zaman & Chang, 2004), which influence N partitioning between the microbial and non-microbial pools (Mooshammer et al., 2014; Niu, Sherry, Zhou, Wan, & Luo, 2010). In addition, warmer temperatures enhance nitrification and denitrification rates thereby affecting soil N pools and N availability to plants. Enhanced nitrification and denitrification can also lead to increased emission of N_2O, a byproduct that is a potent greenhouse gas (~300 times the global warming potential of CO_2 on a 100 year time frame) and contributes to stratospheric ozone depletion (Barnard, Leadley, & Hungate, 2005; Ravishankara, Daniel, & Portmann, 2009).

Soil N cycling processes in terrestrial ecosystems are regulated by microbial functional genes. The *amoA* gene in ammonia-oxidizing bacteria (AOB) and archaea (AOA) regulates inorganic N availability and N_2O production via nitrification, while the *nirK* and *nirS* genes participate in NO_3^- consumption and N_2O production, and the *nosZ* gene mediates conversion of N_2O to N_2 in the denitrification process. Previous studies reported that elevated temperature did not change the abundance of *amoA* genes, or found inconsistent responses of AOA and AOB *amoA* genes to elevated temperature (Liu et al., 2015; Waghmode et al., 2018). Additionally, elevated temperature was found to increase the abundances of *nirK* and *nosZ* genes (Kai et al., 2016; Schölkopf & Smola, 2014; Xue et al., 2016), while *nirS*-containing denitrifiers were reported to be more sensitive to temperature increases than those containing *nirK* and *nosZ* genes (Cui et al., 2015). Although the effects of elevated temperature on soil N cycling processes and relevant genes have been reported by several site-specific studies (Fu, Shen, Zhang, & Zhou, 2012; Ma et al., 2011; Szukics et al., 2010; Xu et al., 2017a, 2017b; Zhang, Li, He, Brookes, & Xu, 2019) and meta-analyses (Bai et al., 2013; Xu & Yuan, 2017), the results vary greatly as a function of ecosystem type and soil management practices. Thus, the response of microbial N cycling processes and gene abundances to elevated temperature at the global scale remains unsettled and requires further investigation. A global synthesis provides a general evaluation of soil N cycling processes in terrestrial ecosystems under elevated temperature and insights for global climate change mitigation and adaptation strategies.

Clarifying the mechanisms mediating microbial N cycling processes under elevated temperature in ecosystems with and without plants on a global scale remains a high priority. In soils without plants, elevated temperature mainly affects microbial abundance, metabolism, enzyme activity and community structure (Davidson & Janssens, 2006; Stone et al., 2012; Tabatabai, 2003; Xue et al., 2016). Given that microbial N transformation is generally influenced by microbial C:N stoichiometry (Cleveland & Liptzin, 2007) and microbial C metabolism is highly responsive to elevated temperature (Dijkstra et al., 2011; Frey, Lee, Melillo, & Six, 2013), changes in N cycling processes under elevated temperature should be intimately coupled with C cycling processes. In contrast, elevated temperatures in soils with plants may increase terrestrial net ecosystem production by affecting plant nutrient availability and growing season length (Dusenge et al., 2018). Plant C input to soil (e.g. through root exudates and above- and below-ground litter input) therefore increases microbial growth, respiration and metabolism by supplying C substrates for microorganisms, inducing a priming effect and possible formation of anaerobic microsites (Kuzyakov, Horwath, Dorodnikov, & Blagodatskaya, 2019). The above changes in C cycling are likely linked with N cycling processes, such as N mineralization and denitrification (Cleveland & Liptzin, 2007; Feng et al., 2019). Therefore, a robust global analysis can elucidate the relationships between microbial N cycling processes and other associated factors, disentangling the associated mechanisms based on the large data set of observed results from individual site-specific studies.

Here we conducted a meta-analysis based on 1,270 observations from 134 publications representing a wide range of global ecosystems and soil management practices that reported the site-specific effects of elevated temperature on soil N cycling processes and related functional genes. Our primary objectives were to answer the following questions: (a) How do soil microbial biomass N, mineralization, nitrification, denitrification and relevant functional genes respond to elevated temperature across a wide range of global terrestrial ecosystems? (b) How do N cycling processes and genes differ between ecosystems with and without plants under elevated temperature? and (c) What are the associated mechanisms mediating microbial N cycling processes?

Given the positive responses of microbial maintenance costs and relevant enzyme activities to elevated temperature, we posit that temperature increases will decrease soil microbial biomass N and increase N mineralization, nitrification and denitrification, with or without the presence of plants. The changes in soil microbial N cycling are likely to be highly associated with soil microbial C cycling. Results from this global analysis enhance our understanding of soil N cycling processes and associated genes in response to a warmer world, and the close linkage between soil microbial C and N cycling in terrestrial ecosystems.

2 | MATERIALS AND METHODS

2.1 | Data collection

We searched the Web of Science database for peer-reviewed papers published between January 1, 1988 and August 18, 2018 using the

search terms 'temperature' OR 'warming' in the title, and 'nitrogen' AND 'soil' in the title, keyword or abstract. Primary studies were initially screened to assess their relevance to soil N cycling as affected by elevated temperature in terrestrial ecosystems. From this screening, appropriate studies were selected according to the following criteria. Studies had to report replicated changes in at least one N cycling variable under elevated temperature, and in the control treatment under the same biotic and abiotic conditions. Field trials and pot experiments with plant growth and laboratory incubations without plant growth were both included in this meta-analysis. For laboratory incubation experiments (34% of our literature sources) using a gradient of temperature treatments, the paired comparison was calculated utilizing the relatively lower temperature as the control (i.e. reference condition) and the higher temperature as the treatment. This designation covers soils with different initial temperatures.

Basic information including site coordinates, ecosystem type, soil and air temperature, presence or absence of plants, water management and experimental duration was extracted from the publications. As 13 studies only reported the place names (e.g. city and reserve) where soil samples were collected rather than specific site coordinates, we estimated the coordinates for these studies by searching the place names in Google Maps. Studies without identified coordinates were marked accordingly in Table S1. If vegetation type or crop growth was reported in the warming experiments, we classified these experiments as 'soils with presence of plants'. Correspondingly, experiments without vegetation type or crop growth were categorized as 'soils without presence of plants'. Data from the control and elevated temperature treatments were extracted for microbial biomass C and N, the rates of microbial N mineralization, nitrification, denitrification, CO_2 emissions and N_2O emissions, N functional genes (e.g. AOA *amoA*, AOB *amoA*, bacterial *nirS*, *nirK*, *nosZ* and 16S gene abundance) and basic soil parameters (e.g. NH_4^+, NO_3^-, dissolved organic C [DOC], and dissolved organic N [DON]). DATA THIEF software was used to extract data presented in figures (Bas Tummer, Eindhoven, the Netherlands), while data from tables and text were directly extracted. The number of studies utilizing DATA THIEF versus direct extraction of values is shown in Table S1. If N transformation dynamics were presented over time in an experiment, we only used the data from the final sampling time as the differences between the control and treatments were relatively constant. If multiple crops or growing seasons in field experiments were available, each crop or growing season was considered as a unique observation. If data were available from multiple soil layers, only data from the surface layer were included. Overall, data from 134 publications with 1,270 observations were included in the meta-analysis. Sample locations and publication information are presented in Supporting Information (Figure S1; Table S1).

2.2 | Data analysis

The effects of elevated temperature on soil N cycling processes and genes were evaluated using the natural log response ratio ($\ln R_i$) as the effect size. The $\ln R_i$ was calculated (Butler, Elser, Lewis, Mackey, & Chen, 2018; Hedges & Olkin, 1985) using the following equation:

$$\ln R_i = \ln(Xe_i/Xc_i) = \ln(Xe_i) - \ln(Xc_i), \quad (1)$$

where Xc_i and Xe_i denote the mean of the N-related variable in control and elevated temperature treatments of the *i*th observation respectively. The variance (V_i) of $\ln R_i$ was calculated by:

$$V_i = \frac{Se_i^2}{Ne_i Xe_i^2} + \frac{Sc_i^2}{Nc_i Xc_i^2}, \quad (2)$$

where Sc_i and Se_i denote the standard deviation (*SD*) of the N-related variable in control and elevated temperature treatments of the *i*th observation respectively. If the *SD* of the control and/or treatments was missing, we generated an estimate using the average coefficient of variation for data sets with known *SD*s (Geisseler & Scow, 2014). The terms Nc_i and Ne_i denote the sample sizes of N-related variables in the control and elevated temperature treatments of the *i*th observation respectively. The mean effect size (mean ln*R*) was calculated from the $\ln R_i$ of individual observations with a random effects model using MetaWin software (Rosenberg, Adams, & Gurevitch, 2000):

$$\text{Mean } \ln R = \frac{\sum_{i=1}^{n} W_i \ln R_i}{\sum_{i=1}^{n} W_i}, \quad (3)$$

where W_i is the reciprocal of sample variance (i.e. $W_i = 1/V_i$) and *n* is the number of observations.

The 95% confidence intervals were calculated and corrected for bias using a bootstrapping procedure with 999 iterations (Dixon, 1993). The mean effect size was considered significant if the bootstrapped confidence intervals did not overlap with zero (Hedges & Olkin, 1985). The effects of elevated temperature on basic soil properties were also calculated using the above procedures. For N_2O and CO_2 emission rates, although some studies were reported in different units (i.e. mg/kg vs. kg/ha), the lack of reported soil bulk density data did not bias the results, as the effect size calculation of the $\ln R_i$ value was based on a ratio in which the bulk density term appears in both the numerator and denominator, thereby cancelling each other out.

To determine the effects of categorical attributes, we calculated the heterogeneity of mean effect sizes between groups using random-effects models, and compared the $Q_{between}$ values to a chi-squared distribution (Rosenberg et al., 2000). The effect of categorical attributes was significant if the $Q_{between}$ value was at $p < .05$. The following categorical variables were assessed: soils with presence/absence of plants, ecosystem type, experimental duration, soil temperature change and water management regime. If air temperature was reported instead of soil temperature, we estimated the corresponding soil temperature based on the regression curve reported in Dwyer, Hayhoe, and Culley (1990). We performed Pearson correlation analysis to examine the relationship between the effect size of CO_2 emissions and the effect sizes for rates of N mineralization,

nitrification, denitrification and N_2O emissions. We conducted Spearman correlation analysis to examine relationships between the effect size of substrate availability (NH_4^+ and NO_3^-) and effect sizes for nitrification and denitrification gene abundances, and the relationship between the effect size of AOA *amoA* and AOB *amoA* abundance.

3 | RESULTS

3.1 | Effect of elevated temperature on soil N cycling

Elevated temperature decreased ($p < .05$) soil microbial biomass N and increased soil N mineralization rate, DON and NH_4^+ concentration, with or without plants (Figure 1; Figure S2). Additionally, elevated temperature increased the rates of soil nitrification and denitrification, with or without plants (Figure 1), leading to increased soil N_2O emissions (Figure 2). The effect size of elevated temperature on soil microbial biomass N was dependent on the presence or absence of plants ($p < .05$), but this was not the case for soil N mineralization, nitrification and denitrification (Figure 1). The effect sizes of N mineralization rate ($r = .55$; $p < .05$) and denitrification rate ($r = .33$; $p < .05$) had positive relationships with the effect size of soil CO_2 emissions, while the effect size of soil nitrification rate ($r = .13$; $p > .05$) showed no relationship with the effect size of soil CO_2 emissions (Figure 3).

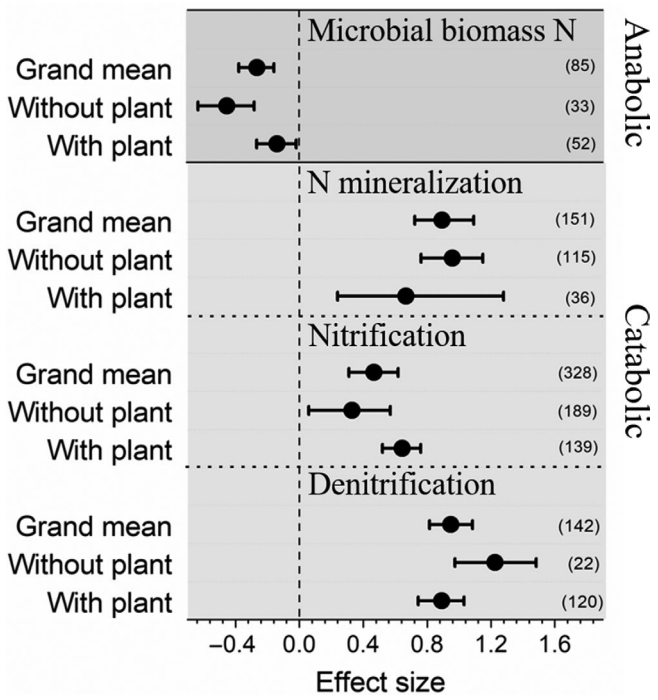

FIGURE 1 Effects of elevated temperature on soil microbial biomass N and rates of N mineralization, nitrification and denitrification, expressed as the mean effect size with bootstrap 95% confidence intervals. Number of observations is in parentheses

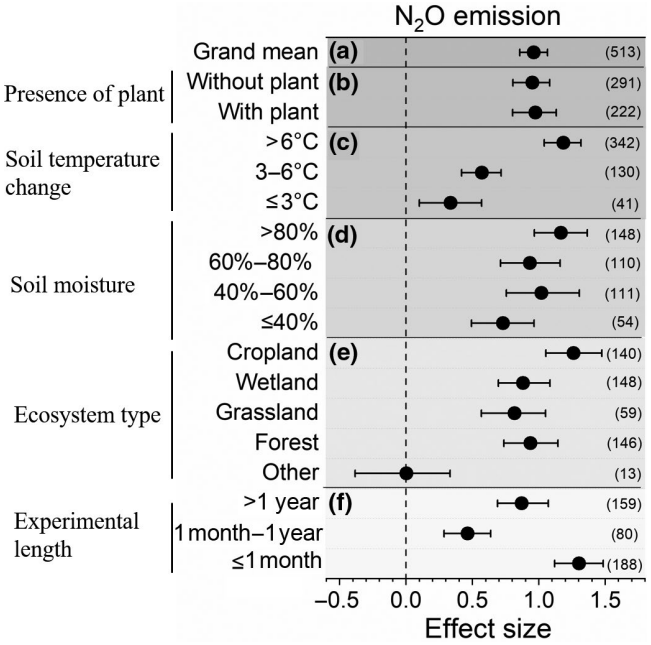

FIGURE 2 Effects of elevated temperature on soil N_2O emission: (a) overall N_2O emission; (b) presence or absence of plants; (c) magnitude of soil temperature change; (d) soil moisture (WFPS, %) classes; (e) ecosystem type; and (f) experimental length, expressed as the mean effect size with bootstrap 95% confidence intervals. Number of observations is in parentheses

3.2 | Effect of elevated temperature on N_2O emissions

Elevated temperature increased ($p < .05$) soil N_2O emission with or without plants (Figure 2a,b). N_2O emissions increased by 40% when the change in soil temperature was <3°C, but increased considerably (up to 227%) when the temperature increase was >6°C (Figure 2c). Emissions of N_2O under elevated temperature increased with increasing soil moisture content and were most sensitive at soil water-filled pore space values above 80% (Figure 2d). N_2O emissions were affected by ecosystem type ($p < .05$) and were more sensitive to elevated temperature in cropland than grassland (Figure 2e). N_2O emission was most sensitive to elevated temperature in short-term studies (<1 month), followed by long-term studies (>1 year; Figure 2f). The effect size of N_2O emissions displayed a positive relationship with the effect size of soil CO_2 emissions ($r = .40$; $p < .05$; Figure 3).

3.3 | Effect of elevated temperature on N cycling functional genes

The effect sizes (mean ln*R*) for elevated temperature on the abundances of N cycling genes were smaller than those for N cycling processes. For instance, the mean ln*R* for denitrification genes (i.e. *nirS*, *nirK* and *nosZ*) was <0.30 (Figure 4), while the mean ln*R* for the denitrification process was >0.89 (Figure 1).

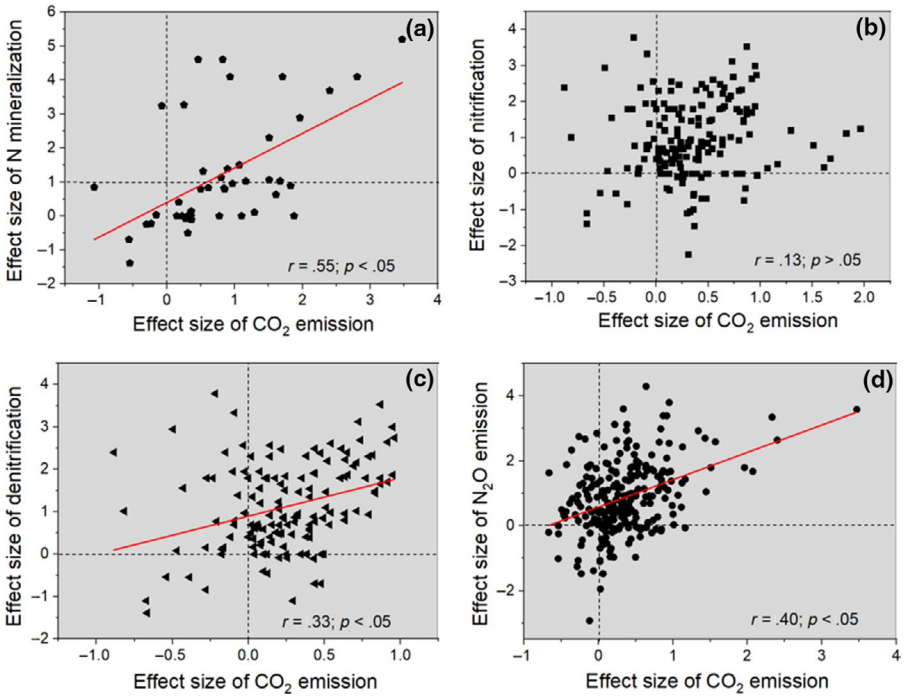

FIGURE 3 Relationships between the effect size of CO_2 emissions and the effect size of (a) soil N mineralization, (b) nitrification, (c) denitrification, and (d) N_2O emissions under elevated temperature [Colour figure can be viewed at wileyonlinelibrary.com]

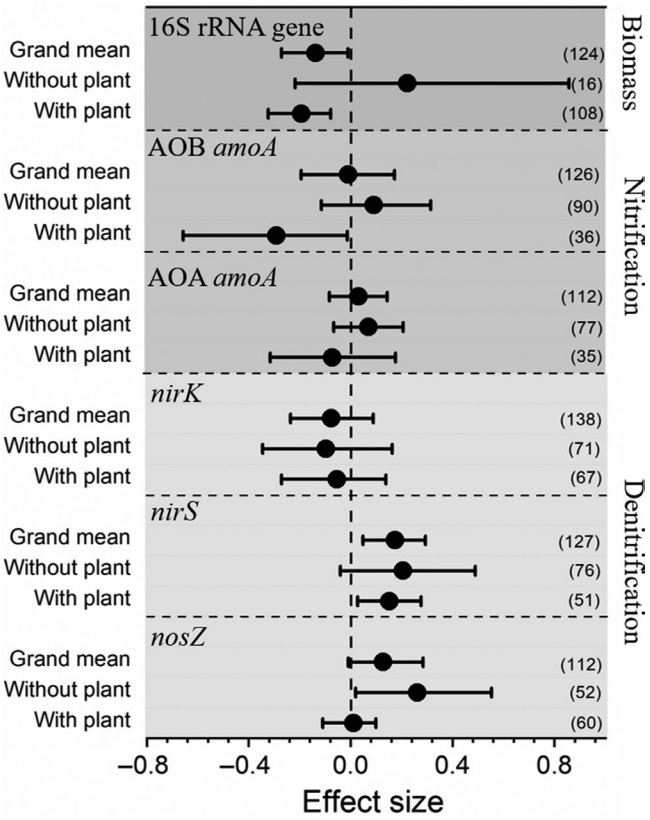

FIGURE 4 Effects of elevated temperature on the abundances of soil 16S rRNA gene and soil N cycling genes: ammonia-oxidizing bacteria (AOB), ammonia-oxidizing archaea (AOA) *amoA*, *nirK*, *nirS* and *nosZ*. Number of observations is in parentheses

Elevated temperature decreased the abundance of *16S* rRNA genes ($p < .05$) in soils with plants, but not in soils without plants (Figure 4). Elevated temperature increased the abundances of the *nirS* gene in soils with plants, while it increased abundances of the *nosZ* gene in soils without plants (Figure 4). However, elevated temperature did not increase the abundances of nitrification genes (AOA and AOB *amoA*) and denitrification gene (*nirK*) with or without plants (Figure 4). The effect size of soil NH_4^+ concentrations had a negative relationship with the effect sizes of the abundance of the AOA *amoA* gene ($r = -.31$; $p < .05$) and AOB *amoA* gene ($r = -.20$; $p < .05$). The effect size of AOA *amoA* gene abundance was negatively correlated with the effect size of AOB *amoA* gene abundance ($r = -.33$; $p < .05$). However, the effect size of soil NO_3^- concentrations had no relationship with the effect sizes of *nirS*, *nirK* and *nosZ* gene abundances (Table 1).

TABLE 1 Relationships between microbial N availability (NH_4^+ and NO_3^- concentrations) and N cycling gene abundances (*AOA amoA*, *AOB amoA*, *nirS*, *nirK* and *nosZ*) under elevated temperature

Comparison	Correlation coefficient (*r*)	Significance (*p*)	Number of observations
NH_4^+ versus *AOA amoA*	−.31	$p < .05$	96
NH_4^+ versus *AOB amoA*	−.20	$p < .05$	101
AOA amoA versus *AOB amoA*	−.33	$p < .05$	113
NO_3^- versus *nirS*	.04	$p = .70$	102
NO_3^- versus *nirK*	.02	$p = .79$	124
NO_3^- versus *nosZ*	.07	$p = .45$	109

4 | DISCUSSION

4.1 | Microbial N cycling processes

The integrated response of microbial N cycling processes to elevated temperature is conceptualized in Figure 5. Notably, elevated temperature drove microbial N cycling from anabolic processes (i.e. speculated from decreased microbial biomass N) to catabolic (i.e. increased N mineralization) processes, regardless of the presence or absence of plants. Thus, less N is converted to microbial biomass and a relatively larger fraction of organic N is released as NH_4^+ by N mineralization. This change leads to increased inorganic N availability (e.g. NH_4^+) and its subsequent processing (e.g. nitrification, denitrification) in the soil environment. The enhanced availability of NH_4^+ under warming will affect the transfer, transport and fate of inorganic N throughout terrestrial ecosystems (Barnard et al., 2005). For instance, increased NH_4^+ under elevated temperature may accelerate nitrification and subsequently denitrification. Given that nitrate has a strong electrostatic repulsion with most soil particles, increased nitrification (converting NH_4^+ to NO_3^-) poses a potential risk for loss of inorganic N via nitrate leaching, contributing to surface and groundwater pollution, and increased denitrification potential (NO_3^- supply). The increased nitrification and denitrification rates are consistent with the increased N_2O emission rates under warming (Figures 1 and 2). The increased N_2O emissions with elevated temperature occurred irrespective of the presence/absence of plants (Figure 2a–c), and may provide a positive feedback to global warming (Griffis et al., 2017).

The response of N_2O emissions to elevated temperature is sensitive to several additional soil environmental factors. Griffis et al. (2017) and Di, Cameron, Podolyan, and Robinson (2014) found that ammonia oxidizers and denitrifiers were more abundant and active under wetter soil conditions, which is consistent with our finding that N_2O emissions were higher under wetter conditions (Figure 2d). Nitrous oxide emission from cropland was more sensitive to elevated temperature as compared to natural ecosystems, such as grasslands (Figure 2e). This may be associated with frequent soil perturbations caused by agricultural activities

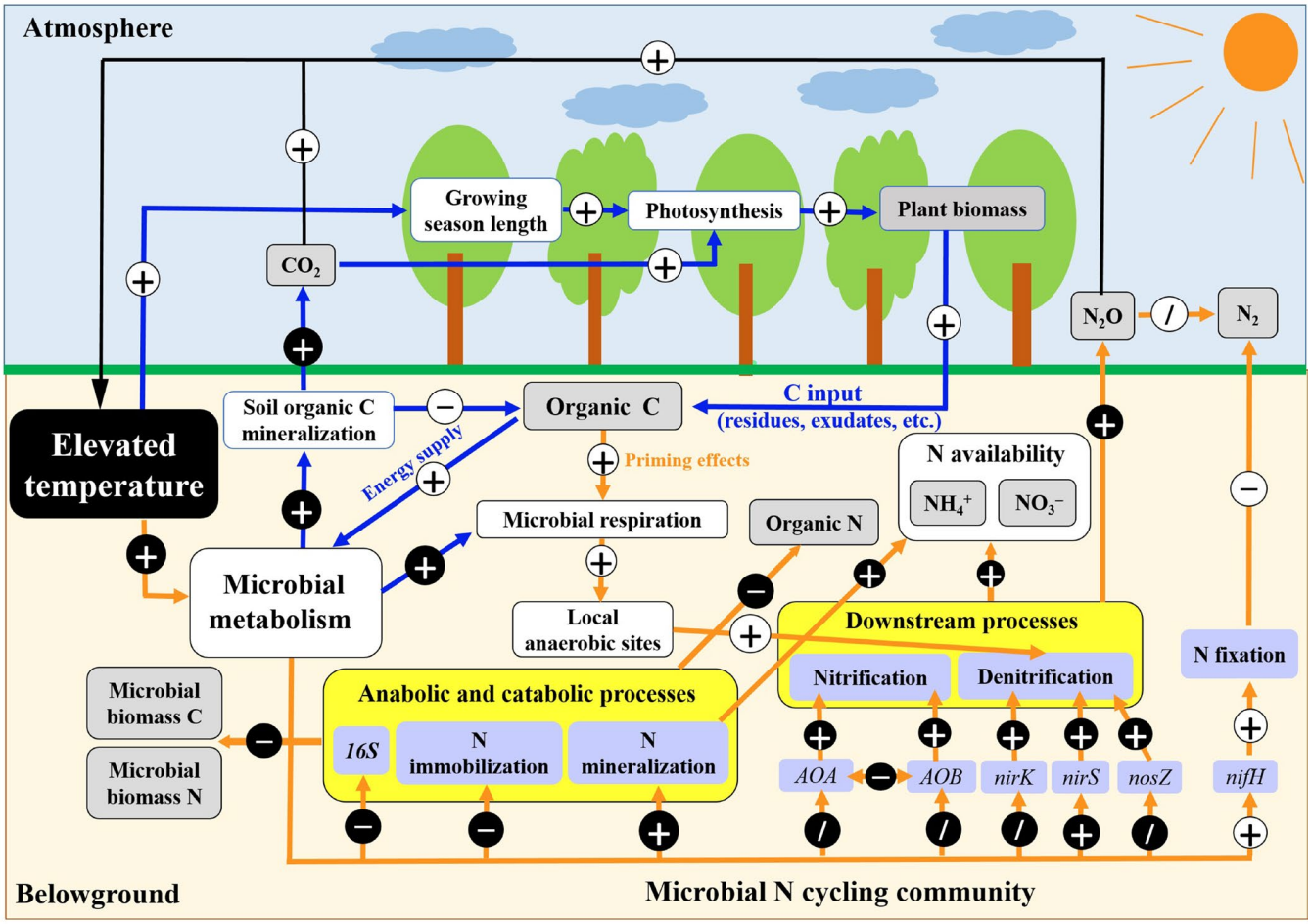

FIGURE 5 Conceptual diagram illustrating how elevated temperature influences N transformation processes and related functional genes. Plant-regulated flows (indirect effects) are indicated by blue arrows, and non-plant-regulated flows (direct effects) are indicated by orange arrows. The symbols "+", "−" and "/" in the circle associated with each arrow represent stimulatory, inhibitory and lack of effect, respectively, on the N transformation process. The black and white circles indicate trends documented in this analysis and in previous studies, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

(e.g. tillage, irrigation, fertilization and harvesting). Perturbations in agricultural ecosystems often lead to large and rapid shifts in microbial community abundance and structure, faster organic C and N turnover rates and increased microbial activity that in turn induce greater N_2O emissions, compared to natural grasslands (Krauss et al., 2017; Prieme & Christensen, 2001). With respect to experimental duration, the largest N_2O emissions occurred in short-term studies (<1 month; Figure 2f). This finding is consistent with several studies showing higher temperature sensitivity of microbial activity in short-term investigations (Grant & Pattey, 2008). Furthermore, N_2O emissions in long-term studies (>1 year) with elevated temperature were greater than for mid-length trials (1 month–1 year). Plant growing season length and soil management practices presumably contribute to these findings (Ganesan et al., 2015).

4.2 | Microbial N cycling genes

Although N cycling gene abundance is assumed to be directly linked with process rates and patterns, the responses of relevant genes to elevated temperature were in some cases inconsistent with those of N cycling processes in our analysis (Figure 5). For instance, the decrease in total *16S* rRNA gene abundance under elevated temperature only occurred in the soils with plants, but not in soils without plants (Figure 4). Furthermore, the increased nitrification rates under elevated temperature were not accompanied by a corresponding increase in the abundance of AOA or AOB *amoA* genes (Figures 1 and 4). We attribute these findings to delayed or no expression of relevant genes, since a number of DNA genes in a stable soil microbial community were dormant or from microbial residues. Sample heterogeneity, seasonal variations, uncertainty of the oxidation rate of nitrite to nitrate and an unknown *amoA*/*16S* rRNA gene ratio also presumably account for some of these inconsistencies.

Despite the lack of changes in nitrification gene abundance, the negative correlations between NH_4^+ concentration and AOA (−0.31) and AOB abundances (−0.20; Table 1) suggest a dependence of microbial nitrification on soil N availability under elevated temperature, but not on microbial C metabolism. In addition, elevated temperature may cause niche differentiation between the AOA and AOB communities (Table 1), adding to our current understanding that AOA and AOB niche differentiation is primarily influenced by initial ammonia availability and soil pH (Prosser & Nicol, 2012). This is likely due to the competition for N substrates between AOA and AOB under warming stress. Our analysis suggests that AOA-AOB niche differentiation preferentially favours the growth of only one type of ammonia oxidizer in a specific ecosystem. Further work targeting temperature-mediated partitioning of AOA and AOB contributions to increased nitrification and N_2O emission is highly warranted.

The abundance of denitrification gene *nirS* was larger than that of autotrophic nitrification gene AOB *amoA* in the presence of plants (Figure 4). This supports the premise that increased C inputs induced by elevated temperature can fuel increased growth of heterotrophic denitrifiers and formation of anaerobic microsites. In addition, the strong relationships between CO_2 emissions and the rates of denitrification and N_2O emissions, along with the lack of correlations between NO_3^- availability and denitrification gene (*nirS*, *nirK* and *nosZ*) abundances found in this analysis, reflect the coupled nature of microbial denitrification and C metabolism (Figure 3; Table 1). Concerning the increased *nirS* gene abundance, with no change in *nirK* gene abundance for soils with plants (Figure 4), we postulate that *nirS* genes are more sensitive to warming and probably contribute more to N_2O production than *nirK* genes. However, fungal *nirK* genes that were not included in this meta-analysis, might also play an important role in N_2O production in terrestrial ecosystems (Laughlin & Stevens, 2002; Lourenço et al., 2018). This premise is based on the purported higher tolerance of fungal *nirK* genes to elevated temperatures (up to 40°C) compared to bacterial *nirK* genes (Xu et al., 2017b). For soils without plants, the increased *nosZ* gene abundance indicates that warming may accelerate the conversion of N_2O to N_2 in the absence of plant C interactions. This also suggests that the response of the *nosZ* gene to elevated temperature is different between ecosystems with and without plants (Figure 4).

4.3 | Mechanisms mediating N cycling processes

4.3.1 | Microbial C and N metabolisms

In spite of the large sample heterogeneity in our global data set, we found that the changing pattern of N anabolic to catabolic processes under soil warming was consistent with the pattern of C metabolic processes (Figure S2). These findings advance our understanding of a microbially regulated coupling of nutrient cycling and plant productivity in terrestrial ecosystems. In particular, microbial N mineralization is highly associated with microbial CO_2 respiration (Figure 3). In general, the microbial C:N stoichiometry is well constrained to a very narrow range across various terrestrial ecosystems. This result is supported by the significant linear correlation between microbial biomass C and N across soils having several orders of magnitude differences in soil microbial C and N concentrations (Cleveland & Liptzin, 2007). Therefore, the well-constrained microbial C:N stoichiometry can empirically explain the consistent responses of C and N anabolic and catabolic processes to elevated temperature across the large data set.

Shifts of microbial N cycling from anabolic process to catabolic process are illustrated in Figure 5 and are likely attributed to: (a) increased microbial maintenance costs (Dijkstra et al., 2011; Frey et al., 2013), and (b) increased relevant enzyme activities under the elevated temperature regimes (Davidson & Janssens, 2006; Oertel, Matschullat, Zurba, Zimmermann, & Erasmi, 2016). From a theoretical perspective, higher temperatures would increase microbial maintenance costs, leading to higher energy demand and lower microbial C use efficiency, that is, the efficiency by which microorganisms convert organic C into biomass C (Dijkstra et al., 2011; Frey et al., 2013; Steinweg, Plante, Conant, Paul, & Tanaka, 2008). This assumption is consistent with the higher microbial respiration and

DOC concentration and the lower microbial biomass C under elevated temperature as determined in this analysis (Figure S2). Due to microbial C:N stoichiometry homoeostasis, microbial N metabolism is strongly linked with microbial C metabolism. Thus, as higher temperature increases microbial maintenance costs, there may be a compensating decrease in microbial biomass N and increased N mineralization as observed in our study. Additionally, the activities of many microbial extracellular enzymes for example, α-glucosidase, β-glucosidase, β-xylosidase and *N*-acetyl-glucosaminidase, consistently increased with increasing temperature within a moderate temperature range (Dijkstra et al., 2011; Stone et al., 2012; Tabatabai, 2003). Increased activity of hydrolytic enzymes that are responsible for changes in C and N metabolism at elevated temperature may in turn lead to increased N mineralization (Davidson & Janssens, 2006; Oertel et al., 2016). However, enzyme deactivation may occur at higher temperatures (>40°C) based on the thermal maxima of enzyme kinetics (Tabatabai, 2003). Thus, we speculate that there will be some inconsistent trends in N cycling processes at extremely high temperatures.

With respect to nitrification, most nitrifiers in terrestrial ecosystems are autotrophic. The lack of a significant correlation between microbial CO_2 respiration and nitrification rate (shown in Figure 3) suggests that nitrification is not directly associated with microbial C metabolism. Alternatively, the enhanced availability of substrate (NH_4^+) by increased N mineralization under soil warming contributed to accelerated nitrification (Table 1). With respect to denitrification, which is mainly regulated by heterotrophic microorganisms, there were positive relationships between microbial CO_2 respiration and the rates of denitrification and N_2O emissions. Together with the lack of a relationship between denitrification gene abundances and NO_3^- concentrations (Figure 3; Table 1), these patterns indicate that microbial C metabolism plays an important role in the acceleration of denitrification under warming temperatures. Specifically, the energy supply and anaerobic sites (i.e. microsites) formed by O_2 depletion and CO_2 production (Harter et al., 2014) caused by microbial C metabolism can lead to an increase in denitrification (Figure 5).

4.3.2 | Plant C inputs to soil

Elevated temperature can indirectly affect N cycling processes in ecosystems with plants by increasing net ecosystem production (Figure S2), in addition to directly altering soil microbial metabolic processes and rates. In the absence of other plant growth limitations, elevated temperature can increase the length of the plant growing season and plant biomass production (summarized in Figure 5), which in turn increases inputs of root exudates and below- and aboveground litter to soils (Dusenge et al., 2018; Richardson et al., 2018). Whether N is incorporated into microbial biomass or released as ammonium to the soil environment depends strongly on the C:N stoichiometry of plant litter/exudate inputs (Mooshammer et al., 2014). A higher C:N of plant litter/exudate inputs to soil than that of the existing soil organic matter would require microorganisms to acquire inorganic N from the soil (i.e. microbial immobilization) to meet their N assimilation needs when processing the plant C inputs (Cleveland & Liptzin, 2007). This could account for the higher microbial biomass N in soils with plants than in soils without plant growth (Figure 1). However, the explanation for the lack of differences in N mineralization rates between ecosystems with and without plants remains unresolved. Our analysis demonstrated that elevated temperature decreased microbial biomass N and increased N mineralization in the presence of plants (Figure 1). We speculate that the larger C input from plants caused by elevated temperature would accelerate microbial growth and enzyme activities, leading to a stronger increase in soil respiration compared to microbial biomass (Kuzyakov et al., 2019).

Given that autotrophic nitrifiers are C substrate-independent (Madigan, Martinko, Dunlap, & Clark, 2008), the lack of a difference in nitrification rates between ecosytems with and without plants (Figure 2) suggests that increased nitrification is likely attributed to the sensitivity of nitrifier enzyme activity to elevated temperature. This assumption is consistent with the findings of Hu et al. (2016) that soil nitrifier activity was strongly affected by elevated temperature. Further support is provided by studies showing no effect of plant C inputs on either autotrophic nitrifiers (Hu et al., 2016) or nitrate reducing microorganisms (Marhan et al., 2011). With denitrification, plant C inputs are an energy source that may directly stimulate the activity and growth of heterotrophic denitrifiers (Moser et al., 2018; Wu et al., 2017). Increased bioavailability of the SOC fraction induced by priming effects may also stimulate the activity of heterotrophic denitrifiers. In addition, the accelerated CO_2 production can form localized sites (i.e. microsites) for anaerobiosis (Harter et al., 2014), creating a necessary environment for denitrification. The positive correlations between microbial CO_2 respiration and the rates of denitrification and N_2O emissions add support for these response pathways (Figure 3).

In conclusion, elevated temperature shifts N cycling from microbial immobilization to enhanced mineralization, nitrification and denitrification pathways across a wide range of global terrestrial ecosystems. The changes in microbial N cycling processes, with the exception of nitrification, are highly associated with microbial C metabolism. Additionally, the presence or absence of plants demonstrated substantial effects on some microbially mediated N cycling processes in response to elevated temperature.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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

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