Received: 9 June 2021 | Accepted: 12 August 2021

DOI: 10.1111/gcb.15851

Global Change Biology WILEY

PRIMARY RESEARCH ARTICLE

Patterns and drivers of global gross nitrogen mineralization in soils

Ahmed S. Elrys[1,2] | Ahmad Ali[1] | Huimin Zhang[1] | Yi Cheng[1,3,4] | Jinbo Zhang[1] | Zu-Cong Cai[1] | Christoph Müller[5,6] | Scott X. Chang[7,8]

[1]School of Geography, Nanjing Normal University, Nanjing, China

[2]Soil Science Department, Faculty of Agriculture, Zagazig University, Zagazig, Egypt

[3]Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, Nanjing, China

[4]Key Laboratory of Virtual Geographic Environment, (Nanjing Normal University), Ministry of Education, Nanjing, China

[5]Institute of Plant Ecology (IFZ), Justus Liebig University Giessen, Giessen, Germany

[6]School of Biology and Environmental Science and Earth Institute, University College Dublin, Dublin, Ireland

[7]Department of Renewable Resources, University of Alberta, Edmonton, Canada

[8]State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Hangzhou, China

Correspondence
Yi Cheng, School of Geography, Nanjing Normal University, Nanjing 210023, China.
Email: ycheng@njnu.edu.cn

Funding information
Financial support for this work was provided by the National Natural Science Foundation of China (42122055, 41977081, 41977032, and 4183064).

Abstract

Soil gross nitrogen (N) mineralization (GNM), a key microbial process in the global N cycle, is mainly controlled by climate and soil properties. This study provides for the first time a comprehensive analysis of the role of soil physicochemical properties and climate and their interactions with soil microbial biomass (MB) in controlling GNM globally. Through a meta-analysis of 970 observations from 337 published papers from various ecosystems, we found that GNM was positively correlated with MB, total carbon, total N and precipitation, and negatively correlated with bulk density (BD) and soil pH. Our multivariate analysis and structural equation modeling revealed that GNM is driven by MB and dominantly influenced by BD and precipitation. The higher total N accelerates GNM via increasing MB. The decrease in BD stimulates GNM via increasing total N and MB, whereas higher precipitation stimulates GNM via increasing total N. Moreover, the GNM varies with ecosystem type, being greater in forests and grasslands with high total carbon and MB contents and low BD and pH compared to croplands. The highest GNM was observed in tropical wet soils that receive high precipitation, which increases the supply of soil substrate (total N) to microbes. Our findings suggest that anthropogenic activities that affect soil microbial population size, BD, soil substrate availability, or soil pH may interact with changes in precipitation regime and land use to influence GNM, which may ultimately affect ecosystem productivity and N loss to the environment.

KEYWORDS
^{15}N isotope dilution technique, climate, ecosystems, gross nitrogen mineralization, microbial biomass, soil properties

1 | INTRODUCTION

Soil nitrogen (N) mineralization is a key microbial process in the global N cycle that controls soil N availability and thus ecosystem productivity (Keuper et al., 2017). The release of reactive N via mineralization activity is also a driver for N losses and is therefore of serious concern in many countries around the world (Galloway et al., 2008). To decrease N losses and increase plant productivity, a sound understanding of the factors that influence the rate of soil N mineralization is required. Most studies on the relationship between plant growth and mineralization at the regional (Fornara et al., 2011; Mueller et al., 2013) or global (Li et al., 2019; Liu et al., 2017; Risch et al., 2019) scale have been based on net N mineralization rather than gross N mineralization (GNM) measurements. As net N

mineralization results from two concurrent and oppositely directed microbial processes (GNM and gross N immobilization) in the absence of plant uptake, measurement of net N mineralization rates does not provide a measure of the true N mineralization capacity of the soil (Davidson et al., 1992). As a result, the net N mineralization rates are usually weakly associated with GNM (Booth et al., 2005; Schimel & Bennett, 2004). Meanwhile, GNM measures the absolute amount of ammonium (NH_4^+) produced from soil organic N due to microbial activity. Given the evidence from terrestrial ecosystems that plants can successfully compete with microbial N immobilization (Inselsbacher et al., 2010; Osterholz et al., 2017), GNM may provide new information about the global potential soil N supply.

The rate of GNM is mainly controlled by soil properties, soil microbes, and climate. For instance, GNM increases with increasing soil organic carbon (C), soil organic N, and soil pH (Cheng et al., 2019; Wang et al., 2016), but decreases with increasing C:N (Cheng et al., 2019). Moreover, changes in soil microbial biomass (MB) have a significant effect on GNM and often positive correlations among GNM and MB (Zeng et al., 2014), and bacterial and fungi abundances (Ribbons et al., 2016) are observed. Furthermore, Zhang et al. (2018) reported that GNM in humid climate regions was significantly greater than that in semiarid and arid regions, reflecting the inherent links between GNM and climate. Moreover, climatic conditions shape soil characteristics over long time scales (Doetterl et al., 2015; Wang, Yoo, et al., 2018). Thus, understanding the role of soil properties, soil microbes, and climate as well as their interactions in controlling GNM globally is necessary for enhancing understanding of potential soil N supply. However, the pattern of GNM at the global scale is still unclear, and only one study on GNM has been done at the global scale (Booth et al., 2005), which mainly focused on the response of GNM to individual soil properties such as total C, total N, C:N, and MB with relatively few observations. They ignored the role of climate, soil pH, and soil physical properties such as soil bulk density (BD) in controlling GNM. Also, they did not test the relationship between controlling factors and GNM across ecosystem types. All of these limitations make it difficult to draw firm conclusions about the global patterns and drivers of GNM.

The current study is the first global analysis on the role of soil physical properties (e.g., BD) and climate (e.g., mean annual precipitation, hereafter referred to as MAP) and their interactions with MB and soil chemical properties in controlling GNM. A better understanding of the direct and indirect factors controlling GNM is needed. It has been reported that changes in MB have a profound influence on GNM (Chi et al., 2021; Zeng et al., 2014). High MB turnover rates (approximately 0.84 $year^{-1}$) support a large release of the readily available substrate (Goyal et al., 1993). Across a wide range of forest ecosystems, Wang, Wang, et al. (2018) suggested MB as an important effector of GNM. Thus, we hypothesize that MB would be the driver of GNM at the global scale (hypothesis 1). At a regional or global scale, BD is usually not considered a dominant predictor of GNM (Booth et al., 2005). Recently, Risch et al. (2019) reported that simulation studies for soil N cycle may benefit from including BD as soil with lower BD is likely to provide micro-soil conditions more favorable for soil microbial thriving. Strong negative correlations of MB (Tan et al., 2005), bacterial and fungi biomass (Li et al., 2002; Smeltzer et al., 1986), total N, and enzyme activities (Dick et al., 1988; Tan et al., 2005) with BD were observed. Therefore, we proposed a new hypothesis that GNM would be dominantly affected by BD at the global scale (hypothesis 2). Moreover, MAP influences soil substrates (Zhao et al., 2017), MB (Serna-Chavez et al., 2013), soil pH (Slessarev et al., 2016), and BD (Mwendera & Feyen, 1994). Low soil moisture reduces soil substrates supply to soil microbes due to limitations in soil substrate diffusion (Borken & Matzner, 2009). Cheng et al. (2014) found that soil microbial respiration decreases with decreasing soil moisture, demonstrating that low soil moisture can decrease microbial activity. Thus, we hypothesize that MAP would be another important factor controlling GNM at the global scale (hypothesis 3). Concurrently, we expect that climate (e.g., MAP) and/or soil properties may indirectly influence GNM through altering MB.

Ecosystem types vary in terms of environmental factors. For instance, soil pH was lower in forests than grasslands and croplands, whereas total C, total N, and MB were higher in forests and grasslands than in croplands (Cookson et al., 2007; Li et al., 2019). Thus, higher GNM was observed in forests than in croplands on a regional scale (Lang et al., 2016). However, the relationship between controlling factors and GNM across ecosystem types at the global scale is not fully obvious. We hypothesize that GNM rates and the relationships between controlling factors and GNM would be ecosystem-specific (hypothesis 4).

To address the above hypotheses, we analyzed data from 337 published papers that include 970 observations. The questions that guided us throughout this analysis were as follows: (i) what are the main drivers of GNM on a global scale? (ii) what are the roles of soil physical properties (e.g., BD) and climate (e.g., MAP) and their interactions with MB and soil characteristics in controlling GNM globally? and (iii) do GNM rates and the relationships between controlling factors and GNM differ among ecosystem types and climatic zones?

2 | MATERIALS AND METHODS

2.1 | Data assembling and overview of data collected

The dataset of GNM was constructed by assembling data from published papers. We screened the articles using the keywords "soil gross nitrogen transformation," "gross nitrogen mineralization," or "^{15}N isotope dilution technique" by the Web of Science Database and Google Scholar up to September 30, 2020. We checked the screened articles to remove duplicate articles. We used the next criteria for assembling data of GNM: (i) GNM was estimated utilizing the topsoil samples (mostly to the top 20 cm soil depth), (ii) the majority of studies were conducted under laboratory incubation conditions, (iii) analyses were restricted to results from unfertilized soils, and (iv) the majority of incubational lengths for GNM range from 24 to 48 h.

A total of 970 observations were collected from 337 papers (Appendix S1) that include data across various ecosystems. The

majority of GNM rates were determined with the ^{15}N isotopic pool dilution technique, but we also used data from ^{15}N tracing studies. Data from organic (139 observations), mineral (751 observations), and mixed (organic + mineral; 80 observations) soil horizons were used in large-scale pattern analysis, but the comparisons among ecosystem types were confined to mineral soil horizons data. Similarly, we included measurements made using both intact and disturbed soils in large-scale pattern analysis, but the comparisons among ecosystem types were confined to disturbed soils data, with the recognition that soil sieving affects GNM (Booth et al., 2005; Gütlein et al., 2016). Moreover, our global analysis revealed no significant differences between the average GNM rates up to 96 h of incubation (Figure S1). Thus, the comparisons among ecosystem types were confined to the data based on incubation periods of 24–96 h.

All original results were assembled from graphs, tables, and text, with unit conversions made as appropriate. The results contained in graphs were generated using GetData (version 2.22). Site-specific data such as latitude, longitude, N deposition, MAP, mean annual temperature (MAT), ecosystem type, climatic zone, BD, soil pH, total C, total N, C:N, dissolved organic C (DOC), dissolved organic N (DON), microbial biomass C (MBC), microbial biomass N (MBN), MBC:MBN, the abundance of fungi and bacteria, fungi: bacteria, soil microbial respiration rate, and net N mineralization were collected from the original papers. We matched these factors with GNM, specific GNM (calculated as GNM÷MBN), and extractable NH_4^+-N. Since GNM reflects both the substrate and MB, the specific GNM, by accounting for the variation in MB size, indicates the availability of quantity and quality of organic N for mineralization (Corre et al., 2003).

In our dataset, MAP and MAT ranged from 266 to 7000 mm, and −4.80 to 28.5°C, respectively. N deposition rate ranged from 2.00 to 82.5 kg N ha^{-1} $year^{-1}$. Soil pH (mostly soil water extract) ranged from 2.80 to 8.80. The observations were distributed across all geographic regions (Figure 1), they are, as Asia (including Russia; 39%), North America (25.5%), Europe (24%), Australia/Oceania (6.3%), South America (3.3%), and Sub-Saharan Africa (1.8%). The dataset considered the ecosystem types: forests, grasslands, and croplands, with 56%, 26%, and 15% of the observations, respectively. In our dataset, climatic zones were coded according to the Köppen Classification System (Kottek et al., 2006) as tropical wet, humid subtropical, marine west coast, the Mediterranean, and continental. Moreover, soil pH is classified according to the United States Department of Agriculture Natural Resources Conservation Service as ultra-acidic (pH < 3.5), extremely acidic (pH 3.5–4.4), very strongly acidic (pH 4.5–5.0), strongly acidic (pH 5.1–5.5), moderately acidic (pH 5.6–6.0), slightly acidic (pH 6.1–6.5), natural (pH 6.6–7.3), slightly alkaline (pH 7.4–7.8), moderately alkaline (pH 7.9–8.4), and strongly alkaline (pH 8.5–9.0).

2.2 | Statistical analyses

Before statistical analyses, the normality of the data was tested using the Kolmogorov–Smirnov test, and all data except soil pH were natural logarithm (ln) transformed to reduce heteroscedasticity.

2.2.1 | Comparison of GNM rates among ecosystem types

We computed the average GNM and specific GNM of each ecosystem type in different climatic zones. We also calculated the average GNM

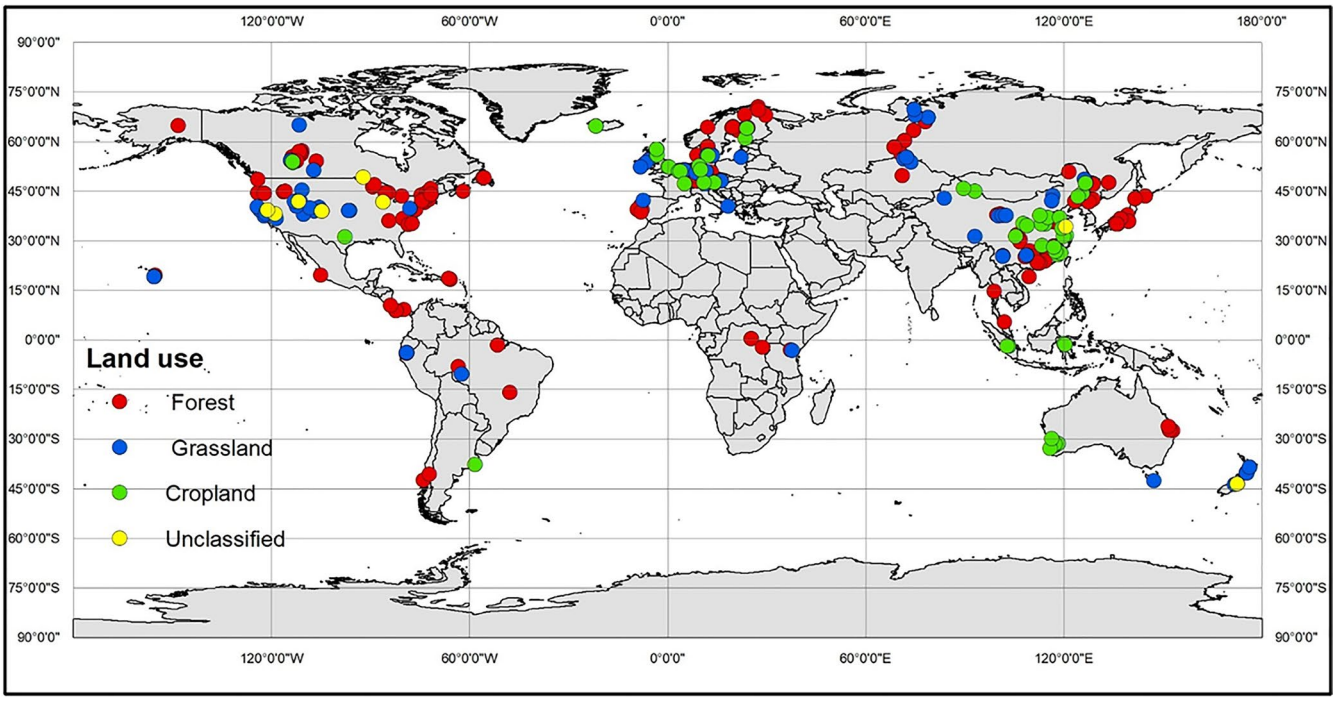

FIGURE 1 Global distribution of study sites included in our study [Colour figure can be viewed at wileyonlinelibrary.com]

and specific GNM of each soil horizon (e.g., organic or mineral soil horizon). Moreover, we calculated the average GNM of each soil pH class in the mineral horizon. The comparisons of GNM and specific GNM across ecosystem types, climatic zones, soil horizons, and soil pH classes were done with Tukey Honestly Significant Difference test by the Statistical Package for Social Sciences (SPSS ver. 23).

2.2.2 | Linear regression analysis

Linear regression analysis using the *"stats"* package in R was employed to analyze global-scale patterns in the data, such as among environmental factors (soil properties, MB, N deposition, or climatic variables) and GNM, specific GNM, and extractable NH_4^+-N.

2.2.3 | Variable selection for mixed-effects meta-regression analysis and structural equation modeling

Variance inflation factors (VIFs) were calculated to examine the presence of collinearities between environmental variables. Environmental variables were excluded when VIF was >5. In summary, we selected the variables to present the soil physical, chemical, and biological properties as well as climatic variables as follows: (i) MB as it is most often thought to control soil N mineralization, (ii) BD as the only soil physical variable of the group and it is easy and inexpensive to measure, (iii) soil total N as the quantity of global total N is the key substrate for soil N mineralization, (iv) soil pH as it influences the size of MB and soil substrates availability, and it is also easy and inexpensive to measure, (v) C:N as biogeochemical processes closely link the N and the C cycles, and (vi) MAP as it is thought to control soil substrates availability and MB, and it is globally available. Because there was no significant relationship between MAT and GNM in linear regression analysis, MAT was not included in our mixed-effects meta-regression analysis and structural equation modeling (SEM), but it was included in our linear mixed-effect model when testing the relationship of GNM with environmental factors across ecosystem types.

2.2.4 | Mixed-effects meta-regression analysis

We tested the impact of MBN, BD, soil pH, total N, C:N, and MAP on GNM in a model of mixed-effects meta-regression using the *"glmulti"* package in R. The importance of each predictor was expressed as the sum of Akaike weights for models that included this factor, which can be considered as the overall support for each variable across all models. A cutoff of 0.8 was set to differentiate between important and unimportant predictors (Terrer et al., 2016).

2.2.5 | Structural equation modeling

We employed SEM to examine how GNM and soil NH_4^+-N availability is affected by soil biological properties (e.g., MBN), soil physical (e.g., BD), and chemical (e.g., soil pH and total N) properties, and/or climate (e.g., MAP). The conceptual SEM (Figure S2) included the direct influences of MBN, BD, total N, soil pH, and MAP on GNM and soil NH_4^+-N availability and the indirect influences where MAP, and/or soil characteristics affected GNM and NH_4^+-N availability via changing MBN. Moreover, the conceptual SEM included the indirect influences of MAP on GNM and NH_4^+-N availability via altering soil physical and chemical properties and the indirect effect of BD on soil chemical properties. SEM testing was performed using the "*lavaan*" package in R. We evaluated the conceptual model by the goodness-of-fit statistics [p-value (χ^2) > .05, comparative fit index = 0.99, and Tucker–Lewis index = 0.91].

2.2.6 | Linear mixed-effect analysis

The relationships of GNM with climatic variables (MAP and MAT), soil properties (BD, pH, total N, total C, and C:N), and MB characteristics (MBC, MBN, and MBC:MBN) across ecosystem types and climatic zones were examined by a linear mixed-effect model. Linear mixed-effect model was performed by the maximum likelihood estimation with the *"lme4"* package in R. For each ecosystem type or climatic zone, the slopes between GNM and variables were assembled and plotted.

3 | RESULTS

3.1 | Global pattern of GNM and specific GNM across ecosystem types and climatic zones

The global average (±standard error) of GNM and specific GNM were 8.63 ± 0.53 mg N kg^{-1} day^{-1} and 84.7 ± 6.30 mg N g^{-1} MBN day^{-1}, respectively. The GNM varied significantly among soil horizons, terrestrial ecosystems, and climatic zones (Figure 2). The average GNM was greater in soil organic horizon than in mineral horizon (Figure 2a). There was also a tendency that GNM was greater in forests and grasslands than in croplands (Figure 2b). The average GNM was greater in the tropical wet region than in other regions (Figure 2c). In continental and marine west coast regions, the average GNM was greater in grasslands than in forests and croplands. However, in tropical wet regions, GNM was greater in forests than croplands and grasslands (Figure S3). There was no significant difference between specific GNM across soil horizons (Figure 2d). Specific GNM was greater in forests than in croplands and grasslands (Figure 2e). The highest specific GNM was observed in the Mediterranean soils (Figure 2f).

3.2 | Effect of environmental factors on GNM rates and N availability

Our study revealed that GNM is driven by MB and dominantly affected by BD and MAP at the global scale, whereby GNM accelerated

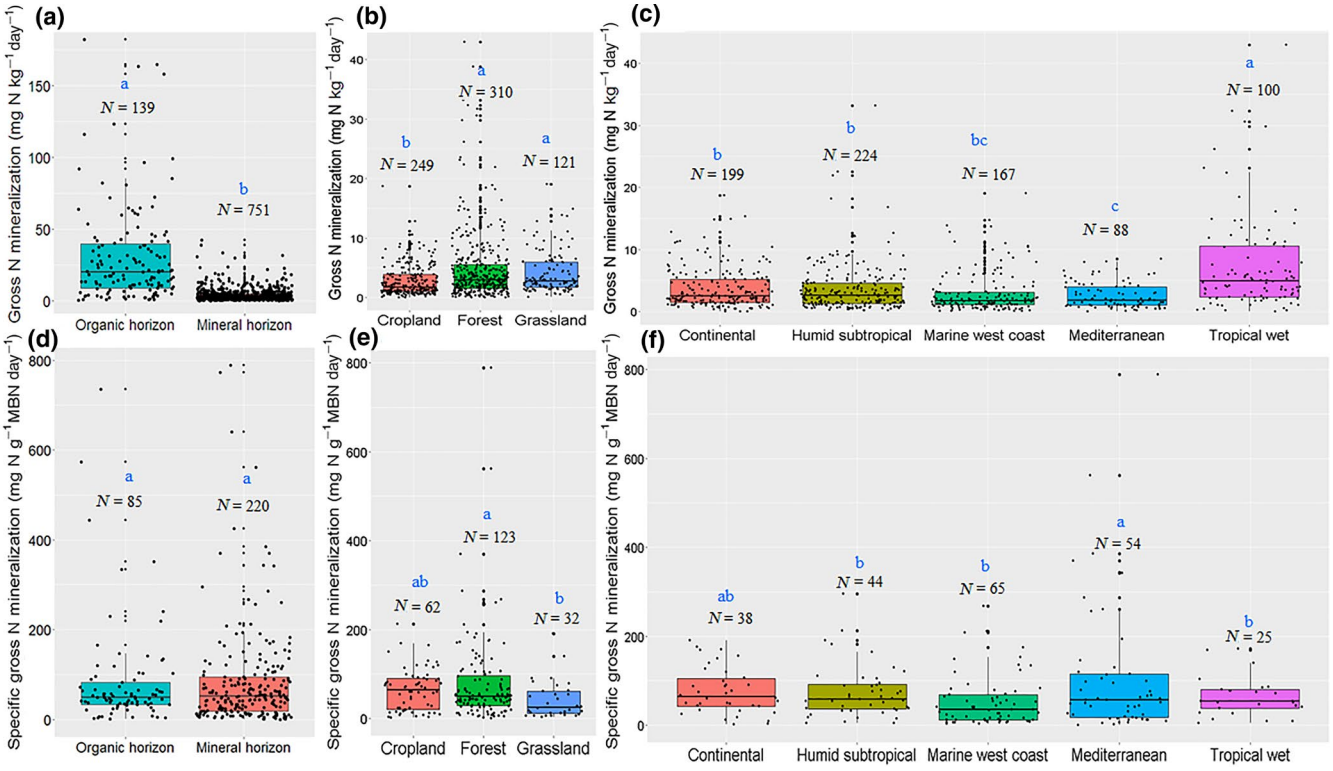

FIGURE 2 Changes (means ± SE) of GNM (a, b, and c) and specific GNM (expressed as GNM per microbial biomass N; d, e, and f) with soil horizons, terrestrial ecosystems, and climatic zones, respectively. The different letters above box plot indicate significant differences at $p < .05$, while *N* is the number of observations. The comparisons among terrestrial ecosystems and climatic zones were confined to mineral soil horizons data. GNM, gross N mineralization; SE, standard error [Colour figure can be viewed at wileyonlinelibrary.com]

as MB and MAP increased but as BD decreased (Figure 3a,b). Moreover, the SEM suggests that higher total soil N and soil pH indirectly accelerated GNM via increasing MB. BD indirectly affects GNM by altering MB, total N, and soil pH (Figure 3b), while MAP indirectly increases GNM by increasing total soil N and decreasing BD. The controlling factors in combination explained for the 57% variation of GNM. The previous relationships were consistent with our linear regression analysis as shown in Figure 4 and Table S2, which also revealed that GNM was positively correlated with total C, C:N, DOC, DON, net N mineralization, bacterial and fungi abundances, and microbial respiration, but was negatively correlated with soil pH, N deposition, and fungi: bacteria.

Moreover, our SEM revealed that GNM, total N, soil pH, and MAP were the main controlling factors of NH_4^+-N availability, whereby available NH_4^+-N increased with increasing GNM and total N, but decreased with increasing MAP and soil pH. The controlling factors in combination explained the 39% variation of available NH_4^+-N. These findings were consistent with our linear regression analysis (Figure 4n; Table S2), which also revealed that extractable NH_4^+-N was related to total soil C, C:N, DOC, DON, and MB. Furthermore, changes in the soil microbial population size were the controlling factor of specific GNM (Table S2). Strong positive correlations (all $p < .001$) among specific GNM and bacterial ($R^2 = .53$) and fungi ($R^2 = .49$) abundances, but negative correlation with fungi: bacteria ($R^2 = .56$) were observed.

3.3 | Relationships of GNM with environmental factors across ecosystem types

Different controlling factors on GNM were operational across terrestrial ecosystems (Figure 5). In croplands, C:N was the driver of GNM, and the MB had a more significant role than the substrates and MAP (Figure 5a). The highest influence on GNM in forests was in the range C:N > total N > MB > total C > MAP > BD (Figure 5b). In grasslands, BD was the driver of GNM, whereas the substrates (total N and total C) had a more significant role than the MB (Figure 5c). The role of MB and substrates in controlling GNM was greater in forests than in grassland and croplands.

The controlling factors of GNM also varied greatly across climatic zones (Figure 6). In continental zones, BD followed by MB and total N were the controlling factors of GNM (Figure 6a). In humid subtropical zones, MAT followed by BD were the controlling factors of GNM, whereas MB had a more significant role than substrates (Figure 6b). In marine west coast zones, BD followed by MAP were the controlling factors of GNM, but the role of total N was greater than that of MB (Figure 6c). In the Mediterranean zones, BD followed by MAT and C:N were the most important factors affecting GNM, but the role of total N was greater than that of MB and soil pH (Figure 6d). The highest influence on GNM in tropical wet zones was in the range MBC:MBN > BD > MBC > total N > total C > MAP > soil pH > MAT (Figure 6e).

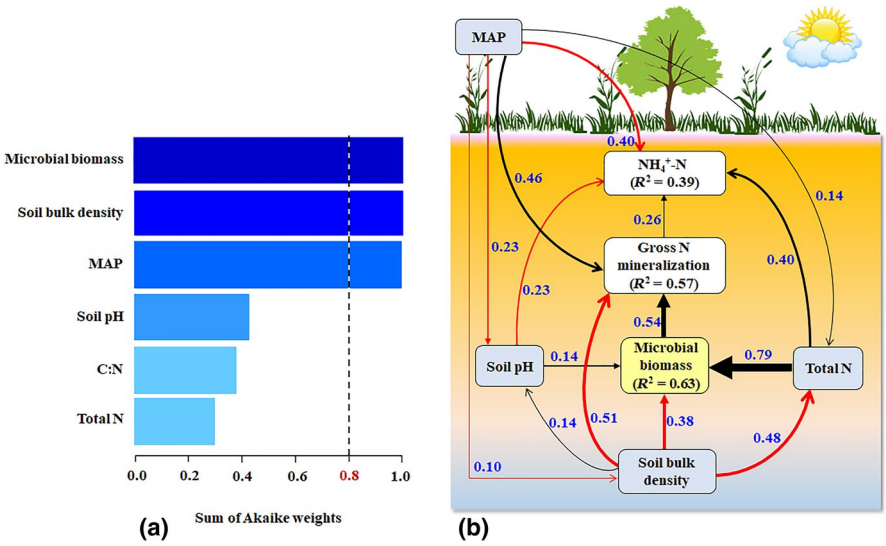

FIGURE 3 (a) Model-averaged importance of the predictors of the effect of the variable on GNM. The importance is based on the sum of Akaike weights derived from model selection using AICc (for small samples). The cutoff is set at 0.8 (dashed line) to differentiate between the important and unimportant predictors. (b) SEM revealing the influences of MAP, soil bulk density, soil pH, total soil N, and MBN on GNM and NH_4^+-N availability. The black arrows indicate significant positive relationships, whereas the red arrows indicate significant negative relationships, where the significance level was set at $\alpha = .05$. Numbers beside the arrows are standardized coefficients. R^2 refers to the variation degree of the variable interpreted by all paths from the combination from the fixed and random effects. AICc, Akaike's Information Criteria corrected; GNM, gross N mineralization; MAP, mean annual precipitation; MBN, microbial biomass N; SEM, structural equation model [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our study provides a comprehensive analysis of the role of BD and MAP and their interactions with MB and soil properties in controlling GNM globally. Former studies on GNM at the global scale mostly focused on the response of GNM to individual soil properties (total N, total C, C:N, and MB) with relatively few observations making it difficult to draw firm conclusions (Booth et al., 2005). For example, Booth et al. (2005) concluded that MB and soil substrate (total C and N) availabilities were all predictive of GNM, but without any details explaining which were the most important and whether both of them directly affected GNM or there were indirect effects. In their study, they neglected the role of BD, soil pH, and climate. Our model selection analysis and SEM showed that GNM was more related to MB, BD, and MAP than soil substrate (total N) and soil pH. However, our SEM suggests that soil pH and total N indirectly influence GNM via altering MB. Our study, for the first time, sheds light on the vital role that BD plays in controlling GNM. Therefore, BD should be included as a key factor controlling GNM in future studies. This detailed understanding will help us achieve firm estimates of soil N availability, and ultimately, ecosystem productivity at global and regional scales.

4.1 | Soil microbes drive GNM at the global scale

Soil microbial biomass played a more significant role in controlling GNM globally than climate (e.g., MAP) and soil physical (e.g., BD) and/or chemical properties (total N, and soil pH). This supports former studies that reported that GNM was best described by MB at the regional scale (Wang, Wang, et al., 2018; Zaman et al., 1999). MB has a rapid turnover rate, ranging from 0.81 to 0.87 $year^{-1}$ (Goyal et al., 1993) and can be considered the driving force behind the N cycle in croplands and natural ecosystems (Inubushi & Acquaye, 2004). The vital role of soil microbes in controlling GNM is probably due to their role in producing soil enzymes (Baldrian, 2014). The depolymerization of complex N-containing organic matter into simple monomers is the first step of N mineralization, and microbial production of exoenzymes drives this process (Darby et al., 2020; Schmidt et al., 2011). MB and enzyme activities (e.g., urease, amidase, deaminase, and chitinase) are closely related (Baldrian, 2014; Mishra et al., 2005; Nayak et al., 2007; Zaman et al., 1999), as are reflected by the close correlations among GNM and MB and enzyme activities (Zaman et al., 1999). Furthermore, the positive relationship between GNM and the abundances of bacteria and fungi (Figure 4j,k) confirmed the important role of MB, most of which are bacteria and fungi (Inubushi & Acquaye, 2004; Yang & Insam, 1991; Yuan et al., 2013), in controlling GNM. We also found that specific GNM is mainly controlled by bacterial and fungal abundances and the bacteria to fungi ratio (Table S2), indicating that soil microbial characteristics are the main factors controlling the quantity of N that is mineralized. Our SEM suggests that soil substrate (total N) is the major determinant of MB, thus influencing GNM. Soils with higher total N usually have greater MB (Table S1) (Kallenbach & Grandy, 2011; Lang et al., 2010), and exhibit faster GNM rates (Booth et al., 2005). For instance, the higher soil substrate availability to soil microorganisms in organic layers caused a greater stimulation of microbial activity, and ultimately

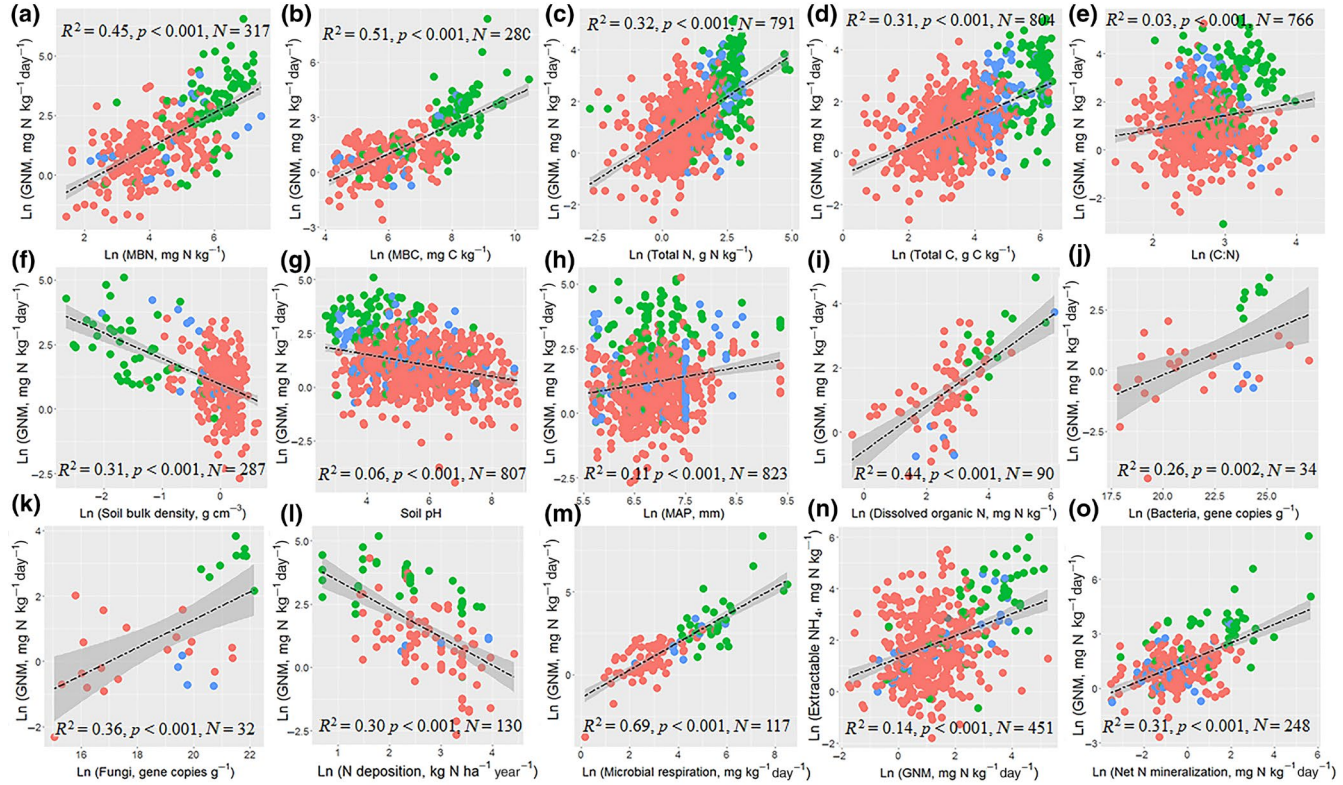

FIGURE 4 Relationship of GNM with MBN (a), MBC (b), total N (c), total C (d), C:N (e), soil bulk density (f), soil pH (g), MAP (h), dissolved organic N (i), bacteria (j) and fungi (k) abundances, N deposition (l), microbial respiration (m), extractable NH_4^+-N (n), and net N mineralization (o) in organic (green dots), mineral (red dots), and mixed (blue dots) soil horizons at the global scale. The gray area refers to the 95% confidence interval around the regression line while *N* is the number of observations. GNM, gross N mineralization; MAP, mean annual precipitation; MBC, microbial biomass C; MBN, microbial biomass N [Colour figure can be viewed at wileyonlinelibrary.com]

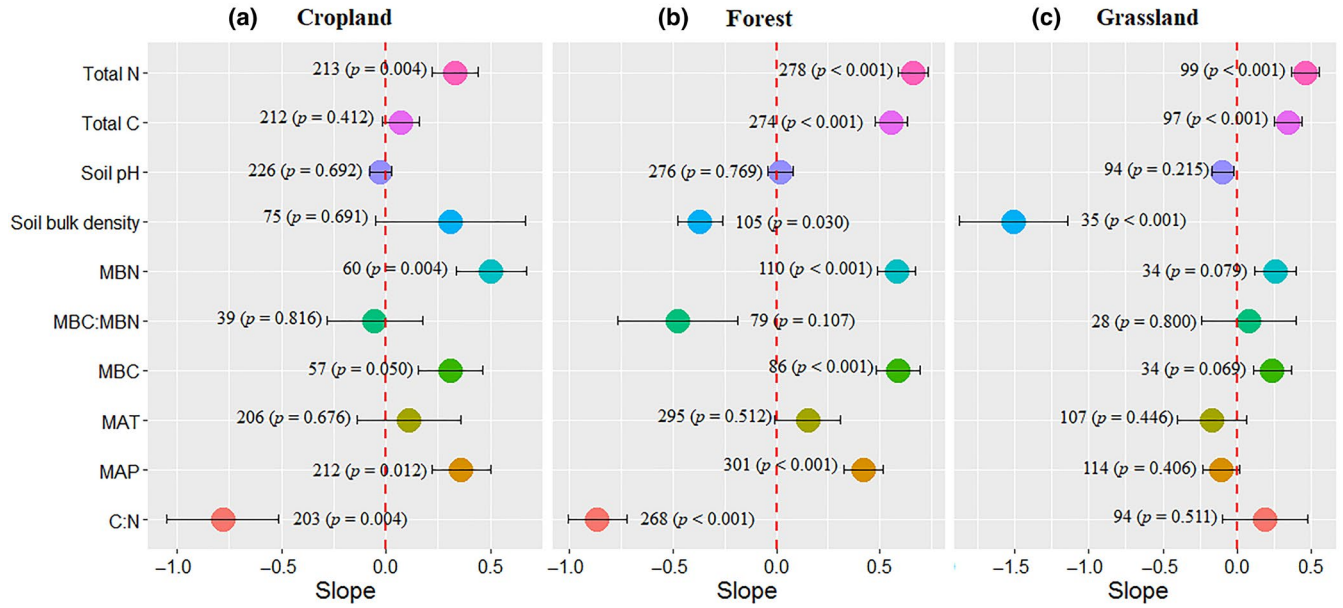

FIGURE 5 The slopes (mean ± SE) of the relationships between GNM rate and environmental factors across terrestrial ecosystems in mineral soil horizons. The values without parentheses are the number of observations. GNM, gross N mineralization; MAP, mean annual precipitation; MAT, mean annual temperature; MBC, microbial biomass C; MBN, microbial biomass N; SE, standard error [Colour figure can be viewed at wileyonlinelibrary.com]

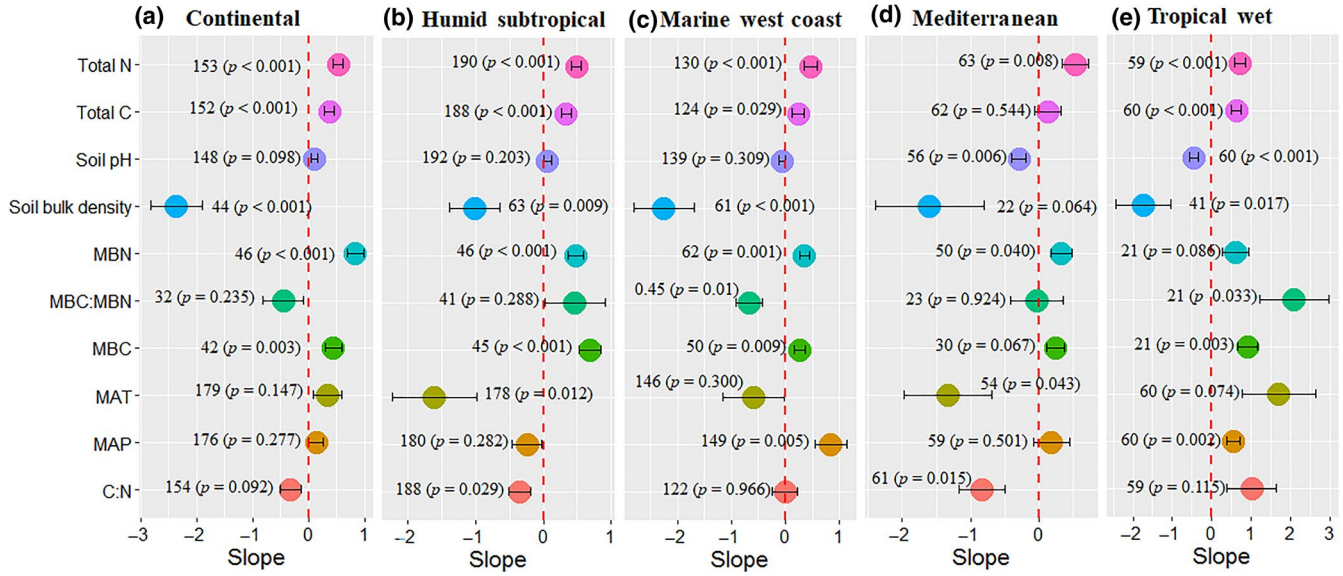

FIGURE 6 The slopes (mean ± SE) of the relationships between GNM rate and environmental factors across climatic zones in mineral soil horizons. The values without parentheses are the number of observations. GNM, gross N mineralization; MAP, mean annual precipitation; MAT, mean annual temperature; MBC, microbial biomass C; MBN, microbial biomass N; SE, standard error [Colour figure can be viewed at wileyonlinelibrary.com]

GNM (Figure 2a), while in mineral horizons, due to the limitation of soil substrate availability, microbial activities were restricted and GNM was reduced (Corre et al., 2010; Sun et al., 2019).

Soil pH is also a major determinant of MB (Priha et al., 2001; Shah et al., 1990). MB increased with increasing soil pH ranging from 3.0 to 7.7 (Aciego Pietri & Brookes, 2008; Cerri & Jenkinson, 1981; Kemmitt et al., 2006; Motavalli et al., 1995). Forest soils treated with ash and lime increased soil pH from 4.0 to 7.0, enhancing bacterial growth fivefold (Bååth & Arnebrant, 1994). However, when soil pH increased from 4.5 to 8.0, the fungal growth decreased by fivefold (Rousk et al., 2009). Interestingly, our findings revealed a strong negative relationship between soil pH and both fungi and bacteria abundances (Figure S5a,b). This partly agrees with Cho et al. (2016), who reported that although an acidic soil (pH 5.2) represented a non-optimal pH for bacterial growth, the bacterial diversity, richness, and evenness in this soil were higher than those found in a neutral pH soil (pH 7.7). These findings may explain the negative relationship between soil pH and GNM at the global scale (Figure 4g). However, further scrutiny showed that this negative relationship is not absolute but had thresholds (Figure S5c). For example, GNM decreased with decreasing soil pH when soil pH was <4.2, likely due to decreased MB and activities (Kemmitt et al., 2006; Motavalli et al., 1995) as a result of the increased availability of heavy metals (Aciego Pietri & Brookes, 2008; Blake et al., 1999). The highest GNM rate was noted in slightly acidic soils (pH 6.1–6.5; Figure S5c), which are ideal for soil microbes, because in this soil plants grow well and produce more root exudates as an available C source for survival and reproduction of microbes (Msimbira & Smith, 2020). Furthermore, although a few studies suggested that GNM is stimulated by increasing soil pH (Cheng et al., 2013; Zhao et al., 2018) due to the increase in soil organic matter solubility (Curtin et al., 1998), we found that GNM significantly decreased when soil pH was >8.0, and the lowest GNM was recorded in strongly alkaline soils (Figure S5c). This may be due to higher pH reduced the activities of the enzymes that directly regulated GNM. For instance, urease (Singh & Nye, 1984) and β-*N*-acetylglucosaminidase (Sinsabaugh et al., 2008) activities reduced when soil pH elevated from 4.0 to 9.0. Therefore, the indirect effect of soil pH on GNM via changing MB and activity should be taken into account.

4.2 | The vital role of soil BD and precipitation in controlling GNM

Interestingly, although the role of BD in controlling GNM is often neglected, we found that BD controls GNM to a degree not much less than MB (Figure 3b), and this finding confirms our second hypothesis. Soils with a low BD would have a high soil porosity, enhancing soil capacity to retain soil water and supply soil oxygen, thus improving soil microbial activity (Ishak et al., 2014). Strong negative associations of MB, total N (Dick et al., 1988), and soil biomass of fungi and bacteria (Li et al., 2002; Smeltzer et al., 1986) with BD were recorded. Soil microbial activity was reduced by 50%–60% with increasing soil compaction (Ishak et al., 2014). Furthermore, soil enzyme activities (e.g., protease) which had close correlations with MB and GNM (Mishra et al., 2005; Zaman et al., 1999) decreased with increasing soil compaction (Li et al., 2002; Tan & Chang, 2007). In contrast to MB and soil substrates quantity and quality, BD is usually not considered a master factor controlling GNM (Booth et al., 2005). Here, we show that BD is a main factor driving GNM. Accordingly, future GNM studies and simulation studies for soil N cycling may benefit from including BD.

Precipitation and its effect on soil moisture can also affect GNM via increasing soil substrates (e.g., total C and N), either via a shift in plant community composition and associated input of litterfall, or by changes resulting from decomposition processes (Zhao et al., 2017). Soils with additional substrates have greater MB on a global scale (Kallenbach & Grandy, 2011; Serna-Chavez et al., 2013). MB increased by 20% with increasing precipitation in grasslands (Liu et al., 2009). High MAP is also a cause of slightly soil acidification (Table S1; Slessarev et al., 2016) because rainwater is slightly acidic (Msimbira & Smith, 2020), stimulating GNM (Figure 3b). Moreover, our SEM revealed that high MAP, which increases biomass production and thus soil organic matter (Zhao et al., 2017), can decrease BD (Herencia et al., 2011), which stimulates GNM. Thus, it is likely that anthropogenic activities affecting soil compaction may interact with future changes in MAP to influence GNM, and ultimately, ecosystem productivity.

4.3 | Relationships of GNM with key factors are ecosystem-specific

Microbial biomass and/or soil substrates (total C and N) are mainly responsible for the GNM variability across terrestrial ecosystems. However, we could see the effect of these factors on GNM was smaller in croplands than in forests. Organic substrates are a main energy source for soil microbes (Schimel & Bennett, 2004). Therefore, a higher quantity of soil substrates can support greater microbial activities, stimulating GNM (Lang et al., 2010). The higher total C content in forests and grasslands (Figure S4) might have contributed to the recorded variations in GNM (Lang et al., 2019). The high specific GNM in forests (Figure 2e) indicates a high-quality substrate is available, supporting high microbial activity (Corre et al., 2006). However, the low specific GNM in croplands (Figure 2e) suggests a decline in activity per unit MB (Corre et al., 2006). Agricultural practices destroy soil structure and enhance soil aeration, accelerating C decomposition (Anderson & Domsch, 2010). Under tillage, MB reduced by 37%–50% (Balota et al., 2004). Moreover, the high inorganic N inputs inhibit humus-degrading enzyme production by soil microbes, and thus decreasing GNM (Corre et al., 2003). We could also note that BD was an important controller of GNM in forests and grasslands, but not in croplands (Figure 5). Soil BD, which is a main negative controlling factor of MB and total N (Figure 3b), was smaller in forests and grasslands than in croplands (Figure S4a). Land-use change from croplands to forests or grasslands significantly increased soil aggregate stability (Delelegn et al., 2017). A well-aggregated soil has high organic matter content and lower BD, stimulating GNM in forests and grasslands (Bizuhoraho et al., 2018). It suggests that management activities that affect soil microbes and soil compaction lessened the relationship among GNM and MB, soil substrate, and BD in croplands. In contrast to what has been observed on a global scale, we found that C:N was a dominant factor controlling GNM in mineral soil horizon of forests and croplands (Figure 5) as GNM increases with decreasing C:N (Booth et al., 2005). Low C:N of organic C substrates supplies a sufficient N to meet the growth and proliferation of the soil microbial community (Cheng et al., 2017; Nguyen et al., 2016). Cheng et al. (2017) proposed a critical C:N of 18, below which organic C substrates could not stimulate microbial N immobilization. The C:N values in our dataset were <18, and thus stimulating GNM.

The average GNM was greater in the tropical wet region than in other regions. In our dataset, tropical wet soils are acidic (pH 3.8–6.53) with relatively high MAT (15.3–28°C) and MAP (1000–5461 mm), stimulating GNM. The higher MAT in tropical zones leads to faster turnover of MB and soil organic matter (Joergensen, 2010). This is in line with the positive relationship between MAT and GNM and the negative relationship between soil pH and GNM in tropical wet regions (Figure 6e). Zhang et al. (2018) reported that GNM in acidic soils in humid regions was significantly greater than that in semiarid and arid regions with a neutral or alkaline pH. However, in the Mediterranean regions, lack of rain and higher MAT, which elevate soil evaporation rate, lead to droughts that cause up to 30% of C resources to be bound in cytoplasmic osmotic protection molecules, negatively influencing soil microbial activity (Aponte et al., 2010). Cytoplasmic osmolytes utilized by bacteria to resist drought stress are amino compounds (Csonka, 1989), whereas fungi utilize polyols that do not contain N (Witteveen & Visser, 1995). Thus, it can be speculated that during drought stress, microbial community composition transformed into a higher abundance of fungi (Aponte et al., 2010), hence reducing GNM (Högberg et al., 2007). GNM has been found to be negatively associated with fungi: bacteria in boreal forests soils (Högberg et al., 2007), and our findings at the global scale also confirmed this negative relationship (Table S2). These results confirm our findings in the Mediterranean regions that the effect of MB and total C on GNM was minor, whereas MAT was a main negative controlling factor.

4.4 | Implications

Understanding the role of soil microbes, soil properties, and climate in controlling GNM is crucial to obtaining a firm conclusion of global soil N availability, which mainly controls the productivity of terrestrial ecosystems. Our findings highlight the vital role of MB, BD, and MAP for controlling GNM and soil N availability globally. In the context of global change, our findings suggest that changes in MB and associated soil properties and climatic variables would ultimately influence soil N availability through changing GNM. Land-use change, particularly the intensification and expansion of croplands, is one of the main causes of global environmental degradation and can severely impact MB, and ultimately, GNM. For instance, converting forests into croplands decreased soil organic matter, total N, and MB (Bizuhoraho et al., 2018; Tellen & Yerima, 2018), and thus reducing GNM (Lang et al., 2019). Furthermore, we found that BD is a key factor controlling GNM, and therefore anthropogenic activities that alter BD would affect GNM rates. For example, soil compaction linked with inappropriate maneuvering of field equipment, and/or

modern cropping systems increases BD, limiting microbial activities and soil substrate availability (Li et al., 2002; Tan & Chang, 2007), and thus reducing GNM and soil N availability. However, organic fertilization, which is a common practice to alleviate soil compaction and enhance soil pore volume size, decreases BD (Xu et al., 2019), stimulating GNM. Over 10 years of organic fertilization, soil BD at a depth of 0–15 cm decreased from 1.6 to 1.2 g cm^{-3} (Herencia et al., 2011), and thus GNM could increase (Zhang et al., 2015).

Nitrogen deposition supplies N for microbial growth and alters soil pH, all of which may influence soil microbial activity, and soil enzyme synthesis, and subsequently GNM (Cheng et al., 2019, 2020). Nitrogen deposition reduced MB by 15% (Treseder, 2008) and might, in turn, reduce GNM (Figure 4l). Moreover, Lu et al. (2013) reported that warming enhanced MB by 2.2%–7.6% from a global synthesis. Thus, global warming may stimulate GNM via increasing MB (Lu et al., 2013). However, global warming is likely to lead to a remarkable increase in evaporative demand, which, when combined with a decrease in MAP in some regions such as the Mediterranean regions, may lead to a shift toward more arid climates (Spinoni et al., 2020), and it can be speculated that GNM would be suppressed based on the positive relationship between MAP and GNM (Figure 3b). Overall, our study indicates that management practices that alter soil microbial population size, BD, soil substrate availability, and/or soil pH may interact with future changes in MAP and MAT to strongly influence the quantity of N that is mineralized, and ultimately, ecosystems productivity. Moreover, the biogeochemical models incorporating BD and climate and its interactions with MB and soil properties will largely enhance the predictability of soil N dynamics under future climate changes.

In our SEM, more than 40% of the variations in GNM are still unexplained, which may be due to shifts in microbial community composition. Our findings revealed that GNM was correlated positively with the abundances of fungi and bacteria ($p < .01$), but negatively with the fungi to bacteria ratio ($p = .001$; Table S2). Unfortunately, soil microbial community structures were not included in our SEM because of insufficient data. In the context of global change, soil microbial community structures are influenced by anthropogenic disturbances such as soil compaction (Ishak et al., 2014) and/ or climate change (Castro et al., 2010), which might lead to changes in GNM and, ultimately, soil N availability. Additionally, soil acidification due to N deposition may increase the fungi to bacteria ratio because of the higher ability of fungi to tolerate high H^+ concentration than bacteria due to their thick and interlinked peptidoglycan cell wall (Zhou et al., 2017), and thus decreasing GNM (Högberg et al., 2007). Hence, future studies addressing the influence of microbial community structure on GNM will improve the confidence in the prediction of available soil N in response to future global changes.

5 | CONCLUSIONS

We identified a number of direct and indirect relationships that can provide a framework to more accurately predict global N cycling. Our findings highlight the importance of MB ultimately driving GNM and increasing soil N availability globally. Precipitation and BD also play a vital role in controlling GNM globally via their direct influences as well as indirect influences via changing MB and total N. Moreover, our SEM suggests that soil pH and total N have indirect influences on GNM via altering MB. The control of MB, total C and total N on GNM was less in croplands and grasslands than in forests. The MAT also is a positive controlling factor of GNM in tropical wet regions, and a negative controlling factor in the Mediterranean regions. Our study highlights that some of the relationships are valid globally but that is also ecosystem-specific should be considered. This framework should help to model more accurately the dynamics of GNM via consideration of easily available variables such MB, BD, MAP, and soil pH under changing climatic conditions and management practices.

CONFLICT OF INTERESTS

The authors declare no competing financial interests.

AUTHORS' CONTRIBUTIONS

Ahmed S. Elrys and Yi Cheng designed the research, collected the data, performed the analysis, and wrote the first draft. All authors contributed to the writing and reviewing of the paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Ahmed S. Elrys https://orcid.org/0000-0003-0373-888X
Yi Cheng https://orcid.org/0000-0002-0559-1319
Christoph Müller https://orcid.org/0000-0001-9107-0044

REFERENCES

Aciego Pietri, J. A., & Brookes, P. C. (2008). Relationships between soil pH and microbial properties in a UK arable soil. *Soil Biology and Biochemistry*, *40*(7), 1856–1861. https://doi.org/10.1016/j.soilbio.2008.03.020

Anderson, T.-H., & Domsch, K. H. (2010). Soil microbial biomass: The eco-physiological approach. *Soil Biology and Biochemistry*, *42*(12), 2039–2043. https://doi.org/10.1016/j.soilbio.2010.06.026

Aponte, C., Marañón, T., & García, L. V. (2010). Microbial C, N and P in soils of Mediterranean oak forests: Influence of season, canopy cover and soil depth. *Biogeochemistry*, *101*(1), 77–92. https://doi.org/10.1007/s10533-010-9418-5

Bååth, E., & Arnebrant, K. (1994). Growth rate and response of bacterial communities to pH in limed and ash treated forest soils. *Soil Biology and Biochemistry*, *26*(8), 995–1001. https://doi.org/10.1016/0038-0717(94)90114-7

Baldrian, P. (2014). Distribution of extracellular enzymes in soils: Spatial heterogeneity and determining factors at various scales. *Soil Science Society of America Journal*, *78*(1), 11–18. https://doi.org/10.2136/sssaj2013.04.0155dgs

Balota, E. L., Colozzi Filho, A., Andrade, D. S., & Dick, R. P. (2004). Long-term tillage and crop rotation effects on microbial biomass and C and N mineralization in a Brazilian Oxisol. *Soil and Tillage Research*, *77*(2), 137–145. https://doi.org/10.1016/j.still.2003.12.003

Bizuhoraho, T., Kayiranga, A., Manirakiza, N., & Mourad, K. A. (2018). The effect of land use systems on soil properties; A case study from Rwanda. *Sustainable Agriculture Research*, *7*(2), 30–40. https://doi.org/10.5539/sar.v7n2p30

Blake, L., Goulding, K., Mott, C., & Johnston, A. (1999). Changes in soil chemistry accompanying acidification over more than 100 years under woodland and grass at Rothamsted Experimental Station, UK. *European Journal of Soil Science*, *50*(3), 401–412. https://doi.org/10.1046/j.1365-2389.1999.00253.x

Booth, M. S., Stark, J. M., & Rastetter, E. (2005). Controls on nitrogen cycling in terrestrial ecosystems: A synthetic analysis of literature data. *Ecological Monographs*, *75*(2), 139–157. https://doi.org/10.1890/04-0988

Borken, W., & Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology*, *15*(4), 808–824. https://doi.org/10.1111/j.1365-2486.2008.01681.x

Castro, H. F., Classen, A. T., Austin, E. E., Norby, R. J., & Schadt, C. W. (2010). Soil microbial community responses to multiple experimental climate change drivers. *Applied and Environmental Microbiology*, *76*(4), 999–1007. https://doi.org/10.1128/AEM.02874-09

Cerri, C., & Jenkinson, D. (1981). Formation of microbial biomass during the decomposition of ^{14}C labelled ryegrass in soil. *Journal of Soil Science*, *32*(4), 619–626. https://doi.org/10.1111/j.1365-2389.1981.tb01734.x

Cheng, Y., Wang, J., Chang, S. X., Cai, Z., Müller, C., & Zhang, J. (2019). Nitrogen deposition affects both net and gross soil nitrogen transformations in forest ecosystems: A review. *Environmental Pollution*, *244*, 608–616. https://doi.org/10.1016/j.envpol.2018.10.054

Cheng, Y., Wang, J., Mary, B., Zhang, J.-B., Cai, Z.-C., & Chang, S. X. (2013). Soil pH has contrasting effects on gross and net nitrogen mineralizations in adjacent forest and grassland soils in central Alberta, Canada. *Soil Biology and Biochemistry*, *57*, 848–857. https://doi.org/10.1016/j.soilbio.2012.08.021

Cheng, Y., Wang, J., Wang, J., Chang, S. X., & Wang, S. (2017). The quality and quantity of exogenous organic carbon input control microbial NO_3^- immobilization: a meta-analysis. *Soil Biology and Biochemistry*, *115*, 357–363. https://doi.org/10.1016/j.soilbio.2017.09.006

Cheng, Y. I., Wang, J., Wang, J., Wang, S., Chang, S. X., Cai, Z., Zhang, J., Niu, S., & Hu, S. (2020). Nitrogen deposition differentially affects soil gross nitrogen transformations in organic and mineral horizons. *Earth-Science Reviews*, *201*, https://doi.org/10.1016/j.earscirev.2019.103033

Cheng, Y., Wang, J., Wang, S.-Q., Zhang, J.-B., & Cai, Z.-C. (2014). Effects of soil moisture on gross N transformations and N_2O emission in acid subtropical forest soils. *Biology and Fertility of Soils*, *50*(7), 1099–1108. https://doi.org/10.1007/s00374-014-0930-y

Chi, Q.-D., Wang, J., Liu, Y.-Q., Zhao, J., Cheng, Y. I., Cai, Z.-C., Feng, X.-J., & Zhang, J.-B. (2021). Varying interactive effects of climate, soil properties, and gross nitrogen dynamics on biomass production between the topsoil and the subsoil in natural grassland ecosystems. *European Journal of Soil Biology*, *104*, https://doi.org/10.1016/j.ejsobi.2021.103299

Cho, S.-J., Kim, M.-H., & Lee, Y.-O. (2016). Effect of pH on soil bacterial diversity. *Journal of Ecology and Environment*, *40*(1), 1–9. https://doi.org/10.1186/s41610-016-0004-1

Cookson, W. R., Osman, M., Marschner, P., Abaye, D. A., Clark, I., Murphy, D. V., Stockdale, E. A., & Watson, C. A. (2007). Controls on soil nitrogen cycling and microbial community composition across land use and incubation temperature. *Soil Biology and Biochemistry*, *39*(3), 744–756. https://doi.org/10.1016/j.soilbio.2006.09.022

Corre, M. D., Beese, F. O., & Brumme, R. (2003). Soil nitrogen cycle in high nitrogen deposition forest: changes under nitrogen saturation and liming. *Ecological Applications*, *13*(2), 287–298. https://doi.org/10.1890/1051-0761(2003)013[0287:SNCIHN]2.0.CO;2

Corre, M. D., Dechert, G., & Veldkamp, E. (2006). Soil nitrogen cycling following montane forest conversion in central Sulawesi, Indonesia. *Soil Science Society of America Journal*, *70*(2), 359–366. https://doi.org/10.2136/sssaj2005.0061

Corre, M. D., Veldkamp, E., Arnold, J., & Wright, S. J. (2010). Impact of elevated N input on soil N cycling and losses in old-growth lowland and montane forests in Panama. *Ecology*, *91*(6), 1715–1729. https://doi.org/10.1890/09-0274.1

Csonka, L. N. (1989). Physiological and genetic responses of bacteria to osmotic stress. *Microbiology and Molecular Biology Reviews*, *53*(1), 121–147. https://doi.org/10.1128/mr.53.1.121-147.1989

Curtin, D., Campbell, C., & Jalil, A. (1998). Effects of acidity on mineralization: pH-dependence of organic matter mineralization in weakly acidic soils. *Soil Biology and Biochemistry*, *30*(1), 57–64. https://doi.org/10.1016/S0038-0717(97)00094-1

Darby, B. A., Goodale, C. L., Chin, N. A., Fuss, C. B., Lang, A. K., Ollinger, S. V., & Lovett, G. M. (2020). Depth patterns and connections between gross nitrogen cycling and soil exoenzyme activities in three northern hardwood forests. *Soil Biology and Biochemistry*, *147*, https://doi.org/10.1016/j.soilbio.2020.107836

Davidson, E. A., Hart, S. C., & Firestone, M. K. (1992). Internal cycling of nitrate in soils of a mature coniferous forest. *Ecology*, *73*(4), 1148–1156. https://doi.org/10.2307/1940665

Delelegn, Y. T., Purahong, W., Blazevic, A., Yitaferu, B., Wubet, T., Göransson, H., & Godbold, D. L. (2017). Changes in land use alter soil quality and aggregate stability in the highlands of northern Ethiopia. *Scientific Reports*, *7*(1), 1–12. https://doi.org/10.1038/s41598-017-14128-y

Dick, R., Myrold, D., & Kerle, E. (1988). Microbial biomass and soil enzyme activities in compacted and rehabilitated skid trail soils. *Soil Science Society of America Journal*, *52*(2), 512–516. https://doi.org/10.2136/sssaj1988.03615995005200020038x

Doetterl, S., Cornelis, J.-T., Six, J., Bodé, S., Opfergelt, S., Boeckx, P., & Van Oost, K. (2015). Soil redistribution and weathering controlling the fate of geochemical and physical carbon stabilization mechanisms in soils of an eroding landscape. *Biogeosciences*, *12*(5), 1357–1371. https://doi.org/10.5194/bg-12-1357-2015

Fornara, D. A., Bardgett, R., Steinbeiss, S., Zak, D. R., Gleixner, G., & Tilman, D. (2011). Plant effects on soil N mineralization are mediated by the composition of multiple soil organic fractions. *Ecological Research*, *26*(1), 201–208. https://doi.org/10.1007/s11284-010-0777-0

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., & Sutton, M. A. (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, *320*(5878), 889–892. https://doi.org/10.1007/s13280-020-01464-z

Goyal, S., Mishra, M., Dhankar, S., Kapoor, K., & Batra, R. (1993). Microbial biomass turnover and enzyme activities following the application of farmyard manure to field soils with and without previous long-term applications. *Biology and Fertility of Soils*, *15*(1), 60–64. https://doi.org/10.1007/BF00336290

Gütlein, A., Dannenmann, M., & Kiese, R. (2016). Gross nitrogen turnover rates of a tropical lower montane forest soil: Impacts of sample preparation and storage. *Soil Biology and Biochemistry*, *95*, 8–10. https://doi.org/10.1016/j.soilbio.2015.12.002

Herencia, J. F., Garcia-Galavis, P. A., & Maqueda, C. (2011). Long-term effect of organic and mineral fertilization on soil physical properties under greenhouse and outdoor management practices. *Pedosphere*, *21*(4), 443–453. https://doi.org/10.1016/S1002-0160(11)60146-X

Högberg, M. N., Chen, Y., & Högberg, P. (2007). Gross nitrogen mineralization and fungi-to-bacteria ratios are negatively correlated in boreal forests. *Biology and Fertility of Soils*, *44*(2), 363–366. https://doi.org/10.1007/s00374-007-0215-9

Inselsbacher, E., Hinko-Najera Umana, N., Stange, F. C., Gorfer, M., Schüller, E., Ripka, K., Zechmeister-Boltenstern, S., Hood-Novotny,

R., Strauss, J., & Wanek, W. (2010). Short-term competition between crop plants and soil microbes for inorganic N fertilizer. *Soil Biology and Biochemistry*, *42*(2), 360–372. https://doi.org/10.1016/j.soilbio.2009.11.019

Inubushi, K., & Acquaye, S. (2004). Role of microbial biomass in biogeochemical processes in paddy soil environments. *Soil Science and Plant Nutrition*, *50*(6), 793–805. https://doi.org/10.1080/00380768.2004.10408539

Ishak, L., McHenry, M. & Brown, P. (2014). Soil compaction and its effects on soil microbial communities in Capsicum growing soil. Paper presented at the XXIX International Horticultural Congress on Horticulture: Sustaining Lives, Livelihoods and Landscapes, (IHC2014), 1123. https://doi.org/10.17660/ActaHortic.2016.1123.17

Joergensen, R. G. (2010) Organic matter and micro-organisms in tropical soils. In P. Dion (Ed.), *Soil biology and agriculture in the tropics. Soil biology* (p. 21). Springer. https://doi.org/10.1007/978-3-642-05076-3_2

Kallenbach, C., & Grandy, A. S. (2011). Controls over soil microbial biomass responses to carbon amendments in agricultural systems: A meta-analysis. *Agriculture, Ecosystems & Environment*, *144*(1), 241–252. https://doi.org/10.1016/j.agee.2011.08.020

Kemmitt, S. J., Wright, D., Goulding, K. W., & Jones, D. L. (2006). pH regulation of carbon and nitrogen dynamics in two agricultural soils. *Soil Biology and Biochemistry*, *38*(5), 898–911. https://doi.org/10.1016/j.soilbio.2005.08.006

Keuper, F., Dorrepaal, E., van Bodegom, P. M., van Logtestijn, R., Venhuizen, G., van Hal, J., & Aerts, R. (2017). Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species. *Global Change Biology*, *23*(10), 4257–4266. https://doi.org/10.1111/gcb.13804

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*(3), 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Lang, M., Cai, Z.-C., Mary, B., Hao, X., & Chang, S. X. (2010). Land-use type and temperature affect gross nitrogen transformation rates in Chinese and Canadian soils. *Plant and Soil*, *334*(1–2), 377–389. https://doi.org/10.1007/s11104-010-0389-z

Lang, M., Li, P., Han, X., Qiao, Y., & Miao, S. (2016). Gross nitrogen transformations in black soil under different land uses and management systems. *Biology and Fertility of Soils*, *52*(2), 233–241. https://doi.org/10.1007/s00374-015-1070-8

Lang, M., Li, P., Ti, C., Zhu, S., Yan, X., & Chang, S. X. (2019). Soil gross nitrogen transformations are related to land-uses in two agroforestry systems. *Ecological Engineering*, *127*, 431–439. https://doi.org/10.1016/j.ecoleng.2018.12.022

Li, C., Ma, B., & Zhang, T. (2002). Soil bulk density effects on soil microbial populations and enzyme activities during the growth of maize (*Zea mays* L.) planted in large pots under field exposure. *Canadian Journal of Soil Science*, *82*(2), 147–154. https://doi.org/10.4141/S01-026

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*(3), 1078–1088. https://doi.org/10.1111/gcb.14557

Liu, W., Zhang, Z., & Wan, S. (2009). Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Global Change Biology*, *15*(1), 184–195. https://doi.org/10.1111/j.1365-2486.2008.01728.x

Liu, Y., Wang, C., He, N., Wen, X., Gao, Y., Li, S., Niu, S., Butterbach-Bahl, K., Luo, Y., & Yu, G. (2017). A global synthesis of the rate and temperature sensitivity of soil nitrogen mineralization: Latitudinal patterns and mechanisms. *Global Change Biology*, *23*(1), 455–464. https://doi.org/10.1111/gcb.13372

Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., Chen, J., Yang, X., & Li, B. O. (2013). Responses of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology*, *94*(3), 726–738. https://doi.org/10.1890/12-0279.1

Mishra, S., Di, H., Cameron, K., Monaghan, R., & Carran, A. (2005). Gross nitrogen mineralization rates in pastural soils and their relationships with organic nitrogen fractions, microbial biomass and protease activity under glasshouse conditions. *Biology and Fertility of Soils*, *42*(1), 45–53. https://doi.org/10.1007/s00374-005-0863-6

Motavalli, P., Palm, C., Parton, W., Elliott, E., & Frey, S. (1995). Soil pH and organic C dynamics in tropical forest soils: Evidence from laboratory and simulation studies. *Soil Biology and Biochemistry*, *27*(12), 1589–1599. https://doi.org/10.1016/0038-0717(95)00082-P

Msimbira, L. A., & Smith, D. L. (2020). The roles of plant growth promoting microbes in enhancing plant tolerance to acidity and alkalinity stresses. *Frontiers in Sustainable Food Systems*, *4*, 106. https://doi.org/10.3389/fsufs.2020.00106

Mueller, K. E., Hobbie, S. E., Tilman, D., & Reich, P. B. (2013). Effects of plant diversity, N fertilization, and elevated carbon dioxide on grassland soil N cycling in a long-term experiment. *Global Change Biology*, *19*(4), 1249–1261. https://doi.org/10.3389/fsufs.2020.00106

Mwendera, E., & Feyen, J. (1994). Effects of tillage and rainfall on soil surface roughness and properties. *Soil Technology*, *7*(1), 93–103. https://doi.org/10.1016/0933-3630(94)90010-8

Nayak, D. R., Babu, Y. J., & Adhya, T. (2007). Long-term application of compost influences microbial biomass and enzyme activities in a tropical Aeric Endoaquept planted to rice under flooded condition. *Soil Biology and Biochemistry*, *39*(8), 1897–1906. https://doi.org/10.1016/j.soilbio.2007.02.003.

Nguyen, T. T., Cavagnaro, T. R., Ngo, H. T. T., & Marschner, P. (2016). Soil respiration, microbial biomass and nutrient availability in soil amended with high and low C/N residue–influence of interval between residue additions. *Soil Biology and Biochemistry*, *95*, 189–197. https://doi.org/10.1016/j.soilbio.2015.12.020

Osterholz, W. R., Rinot, O., Shaviv, A., Linker, R., Liebman, M., Sanford, G., Strock, J., & Castellano, M. J. (2017). Predicting gross nitrogen mineralization and potentially mineralizable nitrogen using soil organic matter properties. *Soil Science Society of America Journal*, *81*(5), 1115–1126. https://doi.org/10.2136/sssaj2017.02.0055

Priha, O., Grayston, S. J., Hiukka, R., Pennanen, T., & Smolander, A. (2001). Microbial community structure and characteristics of the organic matter in soils under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at two forest sites. *Biology and Fertility of Soils*, *33*(1), 17–24. https://doi.org/10.1007/s003740000281

Ribbons, R. R., Levy-Booth, D. J., Masse, J., Grayston, S. J., McDonald, M. A., Vesterdal, L., & Prescott, C. E. (2016). Linking microbial communities, functional genes and nitrogen-cycling processes in forest floors under four tree species. *Soil Biology and Biochemistry*, *103*, 181–191. https://doi.org/10.1016/j.soilbio.2016.07.024

Risch, A. C., Zimmermann, S., Ochoa-Hueso, R., Schütz, M., Frey, B., Firn, J. L., & Seabloom, E. W. (2019). Soil net nitrogen mineralization across global grasslands. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-12948-2

Rousk, J., Brookes, P. C., & Bååth, E. (2009). Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology*, *75*(6), 1589–1596. https://doi.org/10.1128/AEM.02775-08

Schimel, J. P., & Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing paradigm. *Ecology*, *85*(3), 591–602. https://doi.org/10.1890/03-8002

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, *478*(7367), 49–56. https://doi.org/10.1038/nature10386

Serna-Chavez, H. M., Fierer, N., & van Bodegom, P. M. (2013). Global drivers and patterns of microbial abundance in soil. *Global Ecology and Biogeography*, *22*(10), 1162–1172. https://doi.org/10.1111/geb.12070

Shah, Z., Adamst, W., & Haven, C. (1990). Composition and activity of the microbial population in an acidic upland soil and effects of liming. *Soil Biology and Biochemistry*, *22*(2), 257–263. https://doi.org/10.1016/0038-0717(90)90095-H

Singh, R., & Nye, P. (1984). The effect of soil pH and high urea concentrations on urease activity in soil. *European Journal of Soil Science*, *35*(4), 519–527. https://doi.org/10.1111/j.1365-2389.1984.tb00609.x

Sinsabaugh, R. L., Lauber, C. L., Weintraub, M. N., Ahmed, B., Allison, S. D., Crenshaw, C., Contosta, A. R., Cusack, D., Frey, S., Gallo, M. E., Gartner, T. B., Hobbie, S. E., Holland, K., Keeler, B. L., Powers, J. S., Stursova, M., Takacs-Vesbach, C., Waldrop, M. P., Wallenstein, M. D., … Zeglin, L. H. (2008). Stoichiometry of soil enzyme activity at global scale. *Ecology Letters*, *11*(11), 1252–1264. https://doi.org/10.1111/j.1461-0248.2008.01245.x

Slessarev, E., Lin, Y., Bingham, N., Johnson, J., Dai, Y., Schimel, J., & Chadwick, O. (2016). Water balance creates a threshold in soil pH at the global scale. *Nature*, *540*(7634), 567–569. https://doi.org/10.1038/nature20139

Smeltzer, D., Bergdahl, D., & Donnelly, J. (1986). Forest ecosystem responses to artificially induced soil compaction. II. Selected soil microorganism populations. *Canadian Journal of Forest Research*, *16*(4), 870–872. https://doi.org/10.1139/x86-154

Spinoni, J., Barbosa, P., Bucchignani, E., Cassano, J., Cavazos, T., Christensen, J. H., Christensen, O. B., Coppola, E., Evans, J., Geyer, B., Giorgi, F., Hadjinicolaou, P., Jacob, D., Katzfey, J., Koenigk, T., Laprise, R., Lennard, C. J., Kurnaz, M. L., Li, D., … Dosio, A. (2020). Future global meteorological drought hot spots: A study based on CORDEX data. *Journal of Climate*, *33*(9), 3635–3661. https://doi.org/10.1175/JCLI-D-19-0084.1

Sun, L., Xia, Z., Sang, C., Wang, X. U., Peng, B. O., Wang, C., Zhang, J., Müller, C., & Bai, E. (2019). Soil resource status affects the responses of nitrogen processes to changes in temperature and moisture. *Biology and Fertility of Soils*, *55*(6), 629–641. https://doi.org/10.1007/s00374-019-01379-2

Tan, X., & Chang, S. X. (2007). Soil compaction and forest litter amendment affect carbon and net nitrogen mineralization in a boreal forest soil. *Soil and Tillage Research*, *93*(1), 77–86. https://doi.org/10.1016/j.still.2006.03.017

Tan, X., Chang, S. X., & Kabzems, R. (2005). Effects of soil compaction and forest floor removal on soil microbial properties and N transformations in a boreal forest long-term soil productivity study. *Forest Ecology and Management*, *217*(2–3), 158–170. https://doi.org/10.1016/j.foreco.2005.05.061

Tellen, V. A., & Yerima, B. P. (2018). Effects of land use change on soil physicochemical properties in selected areas in the North West region of Cameroon. *Environmental Systems Research*, *7*(1), 1–29. https://doi.org/10.1186/s40068-018-0106-0

Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P., & Prentice, I. C. (2016). Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science*, *353*(6294), 72–74. https://doi.org/10.1126/science.aaf4610

Treseder, K. K. (2008). Nitrogen additions and microbial biomass: A meta-analysis of ecosystem studies. *Ecology Letters*, *11*(10), 1111–1120. https://doi.org/10.1111/j.1461-0248.2008.01230.x

Wang, C., Wang, N., Zhu, J., Liu, Y., Xu, X., Niu, S., Yu, G., Han, X., & He, N. (2018). Soil gross N ammonification and nitrification from tropical to temperate forests in eastern China. *Functional Ecology*, *32*(1), 83–94. https://doi.org/10.1111/1365-2435.13024

Wang, J., Cheng, Y., Zhang, J.-B., Müller, C., & Cai, Z.-C. (2016). Soil gross nitrogen transformations along a secondary succession transect in the north subtropical forest ecosystem of southwest China. *Geoderma*, *280*, 88–95. https://doi.org/10.1016/j.geoderma.2016.06.016

Wang, X., Yoo, K., Wackett, A. A., Gutknecht, J., Amundson, R., & Heimsath, A. (2018). Soil organic carbon and mineral interactions on climatically different hillslopes. *Geoderma*, *322*, 71–80. https://doi.org/10.1016/j.geoderma.2018.02.021

Witteveen, C. F., & Visser, J. (1995). Polyol pools in *Aspergillus niger*. *FEMS Microbiology Letters*, *134*(1), 57–62. https://doi.org/10.1111/j.1574-6968.1995.tb07914.x

Xu, L., Wang, M., Tian, Y., Shi, X., Shi, Y., Yu, Q., & Xie, X. (2019). Changes in soil macropores: Superposition of the roles of organic fertilization and the greenhouse pattern in vegetable plantations. *Soil Use and Management*, *35*(3), 412–420. https://doi.org/10.1111/sum.12490

Yang, J. C., & Insam, H. (1991) Microbial biomass and relative contributions of bacteria and fungi in soil beneath tropical rain forest, Hainan Island, China. *Journal of Tropical Ecology*, *7*(3), 385–393, https://doi.org/10.1017/S0266467400005678

Yuan, H., Ge, T., Zhou, P., Liu, S., Roberts, P., Zhu, H., Zou, Z., Tong, C., & Wu, J. (2013). Soil microbial biomass and bacterial and fungal community structures responses to long-term fertilization in paddy soils. *Journal of Soils and Sediments*, *13*(5), 877–886. https://doi.org/10.1007/s11368-013-0664-8

Zaman, M., Di, H., & Cameron, K. (1999). A field study of gross rates of N mineralization and nitrification and their relationships to microbial biomass and enzyme activities in soils treated with dairy effluent and ammonium fertilizer. *Soil Use and Management*, *15*(3), 188–194. https://doi.org/10.1111/j.1475-2743.1999.tb00087.x

Zaman, M., Di, H., Cameron, K., & Frampton, C. (1999). Gross nitrogen mineralization and nitrification rates and their relationships to enzyme activities and the soil microbial biomass in soils treated with dairy shed effluent and ammonium fertilizer at different water potentials. *Biology and Fertility of Soils*, *29*(2), 178–186. https://doi.org/10.1007/s003740050542

Zeng, Y., Xiang, W., Deng, X., Fang, X., Liu, C., & Peng, C. (2014). Soil N forms and gross transformation rates in Chinese subtropical forests dominated by different tree species. *Plant and Soil*, *384*(1–2), 231–242. https://doi.org/10.1007/s11104-014-2206-6

Zhang, J., Cai, Z., & Müller, C. (2018). Terrestrial N cycling associated with climate and plant-specific N preferences: A review. *European Journal of Soil Science*, *69*(3), 488–501. https://doi.org/10.1111/ejss.12533

Zhang, Y., Wang, F., Zhang, J., Zhu, T., Lin, C., Müller, C., & Cai, Z. (2015). Cattle manure and straw have contrasting effects on organic nitrogen mineralization pathways in a subtropical paddy soil. *Acta Agriculturae Scandinavica, Section B — Soil & Plant Science*, *65*(7), 619–628. https://doi.org/10.1080/09064710.2015.1039054

Zhao, W., Zhang, J.-B., Müller, C., & Cai, Z.-C. (2018). Effects of pH and mineralization on nitrification in a subtropical acid forest soil. *Soil Research*, *56*(3), 275–283. https://doi.org/10.1071/SR17087

Zhao, Y., Ding, Y., Hou, X., Li, F. Y., Han, W., & Yun, X. (2017). Effects of temperature and grazing on soil organic carbon storage in grasslands along the Eurasian steppe eastern transect. *PLoS One*, *12*(10), e0186980. https://doi.org/10.1371/journal.pone.0186980

Zhou, Z., Wang, C., Zheng, M., Jiang, L., & Luo, Y. (2017). Patterns and mechanisms of responses by soil microbial communities to nitrogen addition. *Soil Biology and Biochemistry*, *115*, 433–441. https://doi.org/10.1016/j.soilbio.2017.09.015

SUPPORTING INFORMATION

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

How to cite this article: Elrys, A. S., Ali, A., Zhang, H., Cheng, Y., Zhang, J., Cai, Z.-C., Müller, C., & Chang, S. X. (2021). Patterns and drivers of global gross nitrogen mineralization in soils. *Global Change Biology*, 27, 5950–5962. https://doi.org/10.1111/gcb.15851