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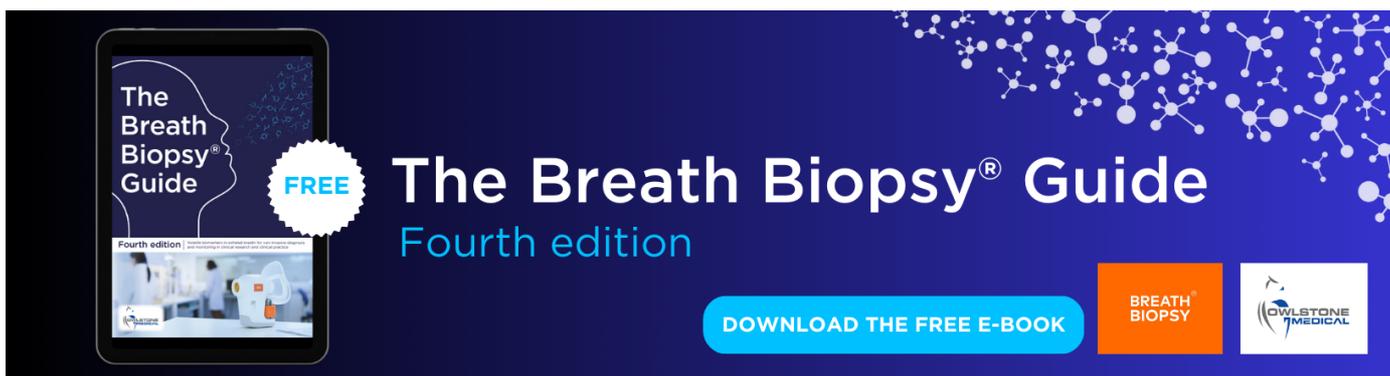
The stoichiometry of soil microbial biomass determines metabolic quotient of nitrogen mineralization

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The stoichiometry of soil microbial biomass determines metabolic quotient of nitrogen mineralization

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Supplementary material for this article is available [online](#)

Abstract

Soil nitrogen (N) mineralization is crucial for the sustainability of available soil N and hence ecosystem productivity and functioning. Metabolic quotient of N mineralization (Q_{\min}), which is defined as net soil N mineralization per unit of soil microbial biomass N, reflects the efficiency of soil N mineralization. However, it is far from clear how soil Q_{\min} changes and what are the controlling factors at the global scale. We compiled 871 observations of soil Q_{\min} from 79 published articles across terrestrial ecosystems (croplands, forests, grasslands, and wetlands) to elucidate the global variation of soil Q_{\min} and its predictors. Soil Q_{\min} decreased from the equator to two poles, which was significant in the North Hemisphere. Soil Q_{\min} correlated negatively with soil pH, total soil N, the ratio of soil carbon (C) to N, and soil microbial biomass C, and positively with mean annual temperature and C:N ratio of soil microbial biomass at a global scale. Soil microbial biomass, climate, and soil physical and chemical properties in combination accounted for 41% of the total variations of global soil Q_{\min} . Among those predictors, C:N ratio of soil microbial biomass was the most important factor contributing to the variations of soil Q_{\min} (the standardized coefficient = 0.39) within or across ecosystem types. This study emphasizes the critical role of microbial stoichiometry in soil N cycling, and suggests the necessity of incorporating soil Q_{\min} into Earth system models to better predict N cycling under environmental change.

Introduction

Soil nitrogen (N) mineralization and N availability largely determine plant productivity and community dynamics (Zak *et al* 2003). The changes in soil N mineralization even determine how an ecosystem responds under climate change (Reich *et al* 2018). As estimated, the amount of N mineralization accounts

for approximately 58% (ranging from 47% to 68% across different ecosystems) of total N demand in a terrestrial biome (Cleveland *et al* 2013). Soil mineralization of organic N is performed by soil microbes at microscale in the concept model (Schimel and Bennett 2004). Moreover, a recent study reveals that soil microbial biomass plays a key role in global soil N mineralization (Li *et al* 2019). It is vital to understand

the microbial role in soil N mineralization for the projection of N cycling. However, it remains elusive what determines the efficiency of N mineralization through soil microbes.

The soil metabolic quotient of N mineralization (Q_{\min}), which is defined as net soil N mineralization per unit of soil microbial biomass N (MBN), is one of the important parameters of soil microbial properties (Anderson and Domsch 1993) and reflects the efficiency of soil microbial N mineralization. Soil Q_{\min} may be influenced by soil microbial biomass and its elemental stoichiometry, climate, as well as soil physical and/or chemical properties. The stoichiometry of microbial biomass varies largely at the regional (Li *et al* 2012) and global scales (Bell *et al* 2014). Sinsabaugh *et al* (2009) point out that stoichiometry of microorganisms, reflecting the relative nutrient limitation for microbial growth, is fundamental for biogeochemical cycles. In terrestrial ecosystems, heterotrophs usually live in a carbon (C)-rich, N-poor condition relative to their physiological requirements (Sistla and Schimel 2012). When the stoichiometric demands of microbial physiology for N are not matched, soil microbes will strive to mine organic N from the environment. Therefore, a higher soil microbial biomass C:N ratio will accompany a higher soil Q_{\min} . The size of soil microbial biomass could also influence soil N mineralization (Li *et al* 2019), which increases with microbial biomass C. Soil Q_{\min} declines with the size of soil microbial biomass as shown in Yellowstone National Park (Tracy and Frank 1998) and following grassland restoration (Rosenzweig *et al* 2016). A general negative relationship between metabolic quotient of C mineralization and the size of soil microbial biomass was discovered with ecosystem development (Wardle and Ghani 2018). There may be a negative relationship between Q_{\min} and microbial biomass C. Climate factors have strong influences on soil N mineralization at the global scale (Liu *et al* 2017). Specifically, soil N mineralization rate increases with higher mean annual temperature (Liu *et al* 2017). The soil physical and/or chemical properties might also regulate soil Q_{\min} . Research discerning the effect of soil texture on soil biogeochemical processes shows that the lowest soil Q_{\min} was found in the clays (Hassink 1994). To our knowledge, the global pattern of soil Q_{\min} and the controls of soil microbial biomass amount and stoichiometry, climate, and soil physical and/or chemical properties on soil Q_{\min} have yet to be quantified. Particularly, how these controlling factors interactively determine soil Q_{\min} remains ambiguous at large spatial scales.

The characteristics of soil N cycling differ among ecosystem types. For example, soil N mineralization is higher in grasslands compared with adjacent croplands (Cookson *et al* 2007). The size of soil microbial biomass C in grasslands and forests is 3.6–6.9 times the size of that in croplands, and the MBN in grasslands and forests is 2.5–4.1 times more than that of

croplands (Liu *et al* 2016). The climatic and soil properties also differ among ecosystems. For instance, soil pH shows significant difference among forests, grasslands, and croplands (Islam and Weil 2000). So, we hypothesized that the controlling factors for soil Q_{\min} would change in different ecosystem types.

In this study, we compiled 871 observations from 79 published articles to address two questions: 1. How do climate, soil physical and/or chemical properties, and soil microbial biomass interactively influence the global variations of soil Q_{\min} ? 2. Which one of the above variables is the dominant driver on the variations of soil Q_{\min} in different ecosystem types?

Materials and methods

Data collection and overview

We retrieved peer-reviewed articles that simultaneously measured the rate of N mineralization and soil microbial biomass in terrestrial ecosystems by the Web of Science (<http://apps.webofknowledge.com>) and China National Knowledge Infrastructure Database (<http://cnki.net>) till 30 July, 2018. We also retrieved articles using Google Scholar. The terms for searching articles were '(nitrogen mineralization OR N mineralization) AND (microbial biomass)'. Duplicates of article were removed. The criteria for selecting eligible articles include: 1. the net N mineralization and MBN were simultaneously reported (approximately only 30% articles on soil N mineralization were eligible); 2. the study was conducted with the upper soil layer (mostly to the 15 cm soil depth); 3. the condition of soil incubation, in particular the temperature of incubation, was available. For each study, we also extracted the number of replications of soil incubation. Site-specific data were also collected from original articles, including geographic information (latitude, longitude), climatic factors (mean annual temperature, mean annual precipitation), soil physical and chemical properties (the content of clay and sand, soil pH), the substrate features (soil organic C, total soil N, and the ratio of soil C to N), and the characteristics of soil microbial biomass (soil microbial biomass C and the C:N of soil microbial biomass). All data were directly extracted from the text, tables, and figures with the latter extracted by GetData Graph Digitizer (version 2.22). When the climatic factors were unavailable in the original article, they were derived from climatic database (<http://worldclim.org/>) with grid precision of $0.5 \times 0.5^\circ$ according to geographic information (i.e. latitude and longitude).

The final dataset of Q_{\min} comprised 871 observations from 79 published articles. The dataset encompassed four types of terrestrial ecosystems and included croplands (292 observations), forests (238 observations), grasslands (147 observations), and wetlands (52 observations) (figure 1(a)). The spatial pattern of observations was: 306 from Asia, 160 from Europe, 101 from Australia, 99 from North America,

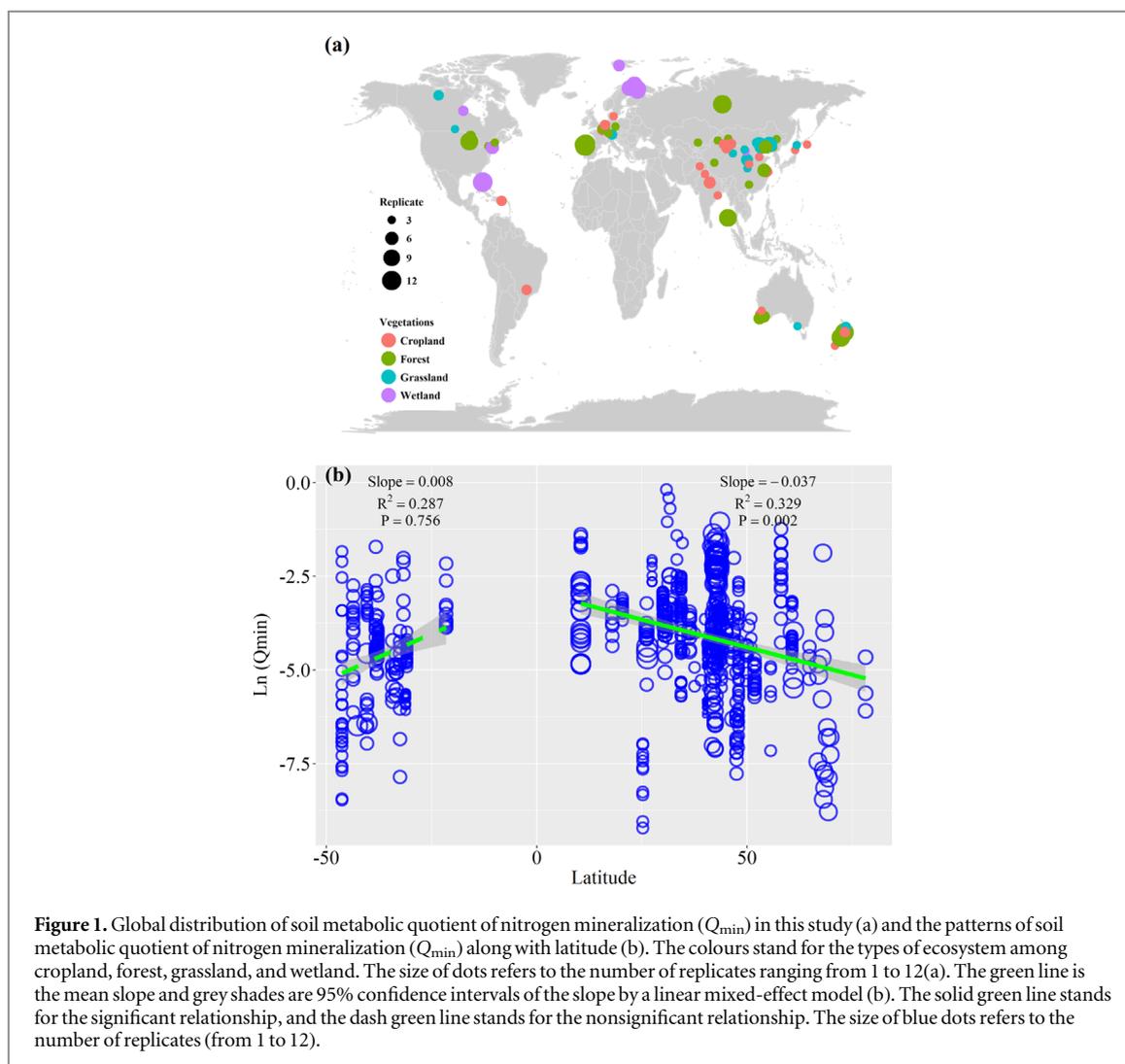


Figure 1. Global distribution of soil metabolic quotient of nitrogen mineralization (Q_{\min}) in this study (a) and the patterns of soil metabolic quotient of nitrogen mineralization (Q_{\min}) along with latitude (b). The colours stand for the types of ecosystem among cropland, forest, grassland, and wetland. The size of dots refers to the number of replicates ranging from 1 to 12(a). The green line is the mean slope and grey shades are 95% confidence intervals of the slope by a linear mixed-effect model (b). The solid green line stands for the significant relationship, and the dash green line stands for the nonsignificant relationship. The size of blue dots refers to the number of replicates (from 1 to 12).

10 from South America, and the others without geographic coordinates. The range of mean annual temperature varied from -2.2°C to 30.1°C , and the range of mean annual precipitation was from 85 to 3100 mm. The soil pH ranged from 3.5 to 9.1, and the content of soil clay from 2.0% to 75.2%.

Data analyses

To calculate the soil Q_{\min} , we adjusted the N mineralization to reference temperature (Xu *et al* 2017), i.e. 25°C , as the majority (525 out of 871 observations) of soil N mineralization were measured at 25°C . All N mineralization rates were standardized on the basis of the Q_{10} of N mineralization, similar to Liu *et al* (2017), using the following formula:

$$N_{\min 2}/N_{\min 1} = Q_{10}^{(25-T_1)/10}, \quad (1)$$

where $N_{\min 1}$ and $N_{\min 2}$ are the original soil N mineralization and adjusted N mineralization at 25°C , respectively. T_1 is the measured temperature for $N_{\min 1}$.

We calculated soil Q_{\min} similarly to the metabolic quotient of soil respiration by Xu *et al* (2017).

$$Q_{\min} = N_{\min 2}/MBN, \quad (2)$$

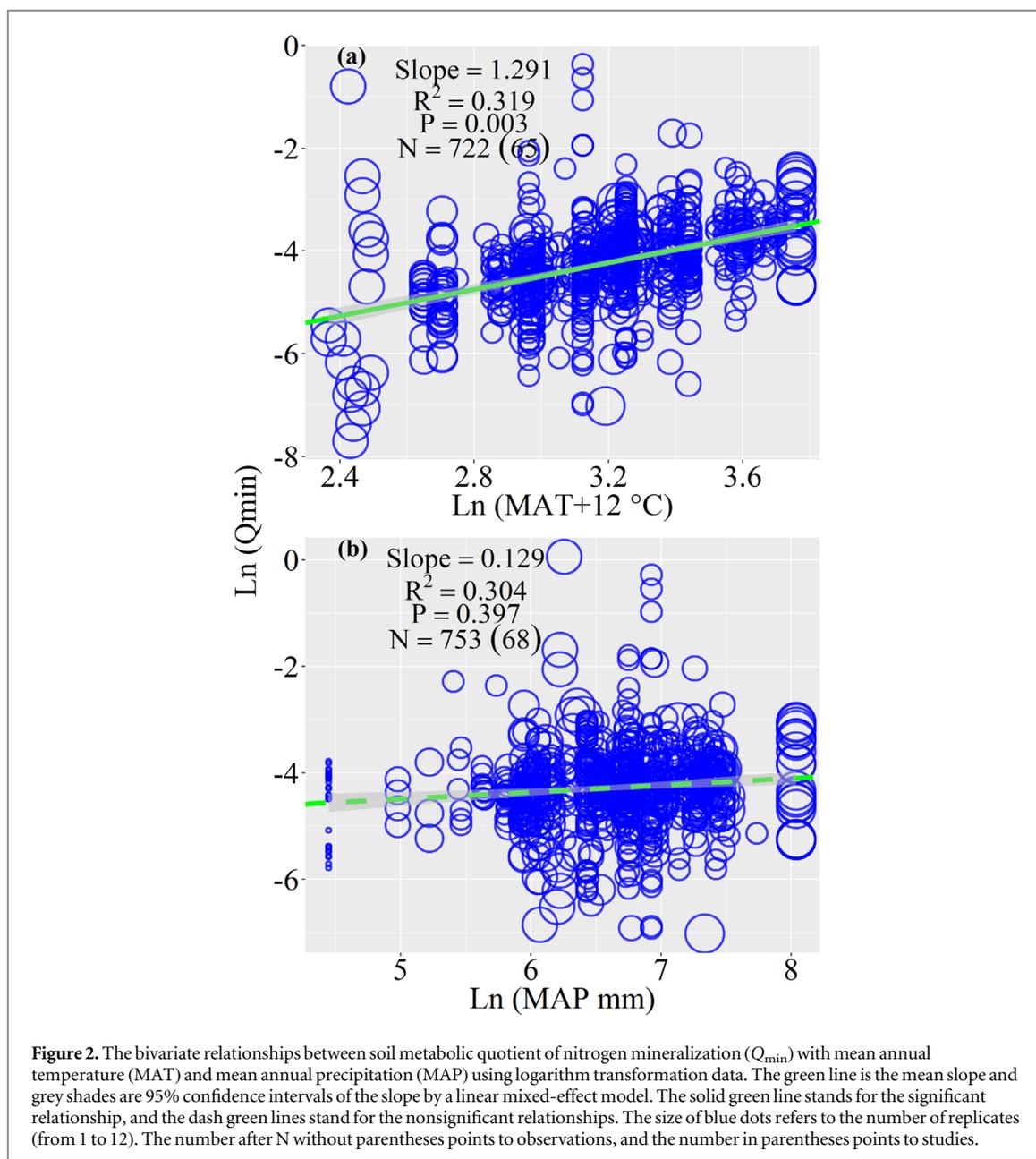
where Q_{\min} is the metabolic quotient of net soil N mineralization, $N_{\min 2}$ is the net N mineralization rate at 25°C , and MBN is the soil MBN.

We examined the patterns of soil Q_{\min} and its controlling factors at a global scale using a linear mixed-effect model. Firstly, we tested the patterns of soil Q_{\min} along latitude and longitude, and then we explored the relationships between soil Q_{\min} and the controlling factors. The model was used as:

$$\ln(Q_{\min}) = \beta_0 + \beta_1 \times \ln X + \pi_{study} + \varepsilon, \quad (3)$$

where β_0 , β_1 , π_{study} and ε are the intercept, slope coefficient, the random effect, and sampling error, respectively. The random effect took the autocorrelation among observations within each 'study' into account. The bivariate relationships between $\ln(Q_{\min})$ and variable were presented as the intercept (β_0) plus coefficient (β_1) times variable plus residuals (ε).

Secondly, the relationship between soil Q_{\min} and each environmental factor was examined in each ecosystem type. All data were standardized using z score normalization in each ecosystem, and the relationships were tested by equation (3). The slope \pm its 95% confidence intervals of each relationship were



graphically presented. All statistical analyses were conducted with R (version 3.5.0., R Development Core Team, Vienna, Austria).

Thirdly, structural equation modelling (SEM) was used to explore the multivariate relationships between soil Q_{min} and environmental factors using the normalized data. Initially, we constructed the conceptual SEM, where the climatic factors (mean annual temperature, mean annual precipitation), soil properties (soil pH and the content of soil clay), the substrate (the content of soil N and the ratio of soil C to N), and the properties of soil microbial biomass (soil microbial biomass C and the C:N ratio of soil microbial biomass) might be directly related to soil Q_{min} . There were also relationships among the environmental factors. For instance, the properties of soil microbial biomass might be influenced by climatic factors and soil properties. The conceptual SEM was tested with the

piecewiseSEM package (Lefcheck 2016). To prevent overfitting, we removed variables, e.g. mean annual precipitation, that were not significantly related to soil microbial biomass C, the C:N ratio of soil microbial biomass, and soil Q_{min} . The optimal SEM was chosen with the lowest Akaike Information Criterion value.

Results

Bivariate relationships of Q_{min} with latitude, climatic variables, soil properties, and microbial biomass at a global scale

Soil Q_{min} was the highest at the equator and tended to decrease with the increasing latitude in both Northern ($r^2 = 0.33$, $P = 0.002$; figure 1(b)) and Southern Hemisphere ($r^2 = 0.29$, $P = 0.756$). There was no significant relationship between Q_{min} and longitude

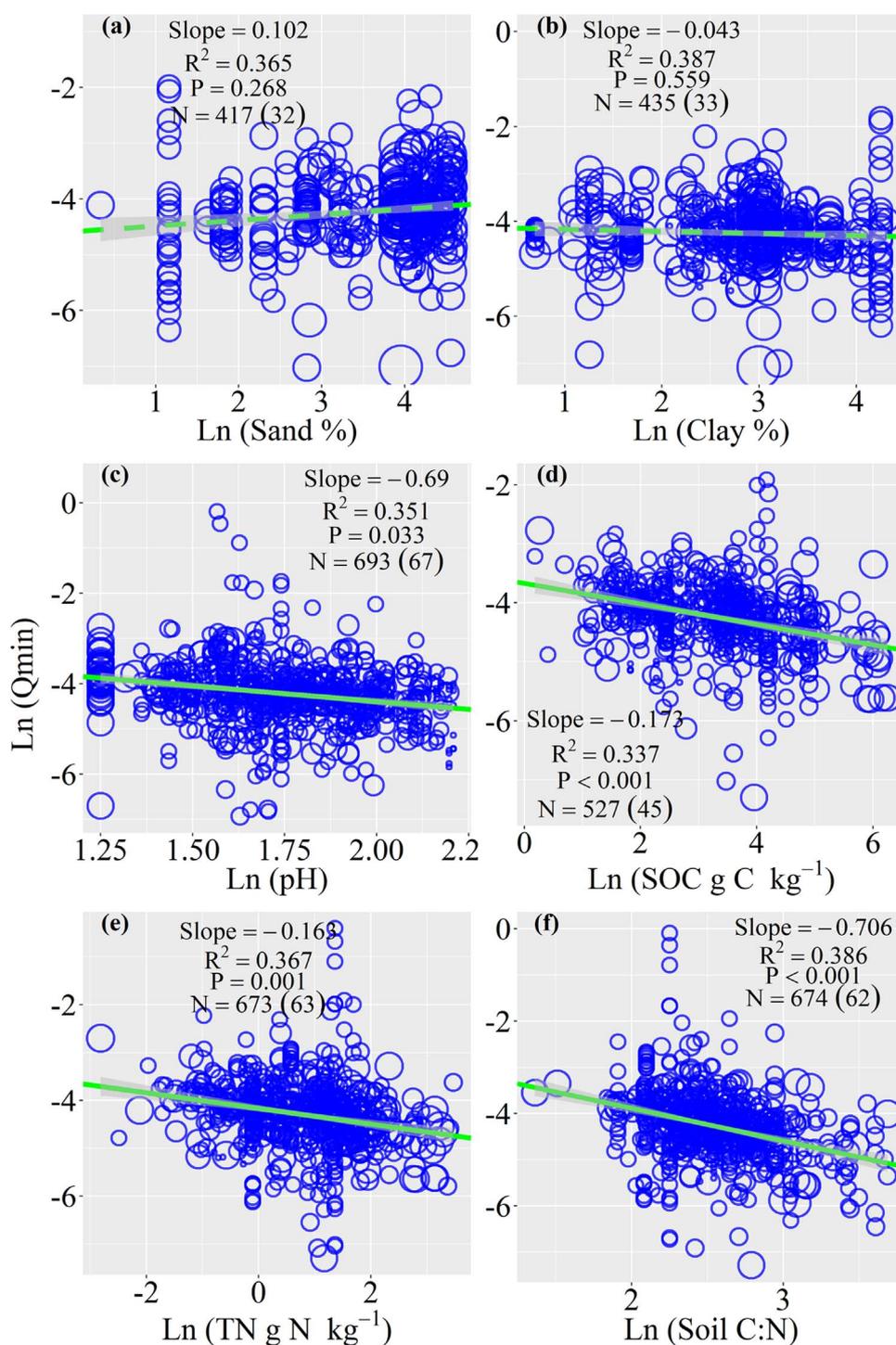


Figure 3. The bivariate relationships between soil metabolic quotient of nitrogen mineralization (Q_{\min}) with the content of soil sand and clay, soil pH, soil organic matter (SOC), total soil nitrogen (TN), and the ratio of soil carbon to nitrogen (soil C:N) using logarithm transformation data. The green line is the mean slope and grey shades are 95% confidence intervals of the slope by a linear mixed-effect model. The solid green line stands for the significant relationship, and the dash green lines stand for the nonsignificant relationships. The size of blue dots refers to the number of replicates (from 1 to 12). The number after N without parentheses points to observations, and the number in parentheses points to studies.

($r^2 = 0.32$, $P = 0.319$; figure S1 is available online at stacks.iop.org/ERL/15/034005/mmedia).

Soil Q_{\min} increased with mean annual temperature with the slope being 1.29 ($r^2 = 0.32$, $P = 0.003$; figure 2(a)), but did not significantly change with mean annual precipitation ($r^2 = 0.30$, $P = 0.397$; figure 2(b)). Soil Q_{\min} decreased with soil pH ($r^2 = 0.35$, $P = 0.033$;

figure 3). Soil Q_{\min} was slightly higher in soils with higher content of sand, and slightly lower with higher contents of clay, but the relationships of Q_{\min} with soil sand or clay contents were not statistically significant ($r^2 = 0.37, 0.39$; $P = 0.268, 0.559$; respectively).

Soil Q_{\min} was significantly related to the properties of the substrate and microbial biomass. Specifically, soil

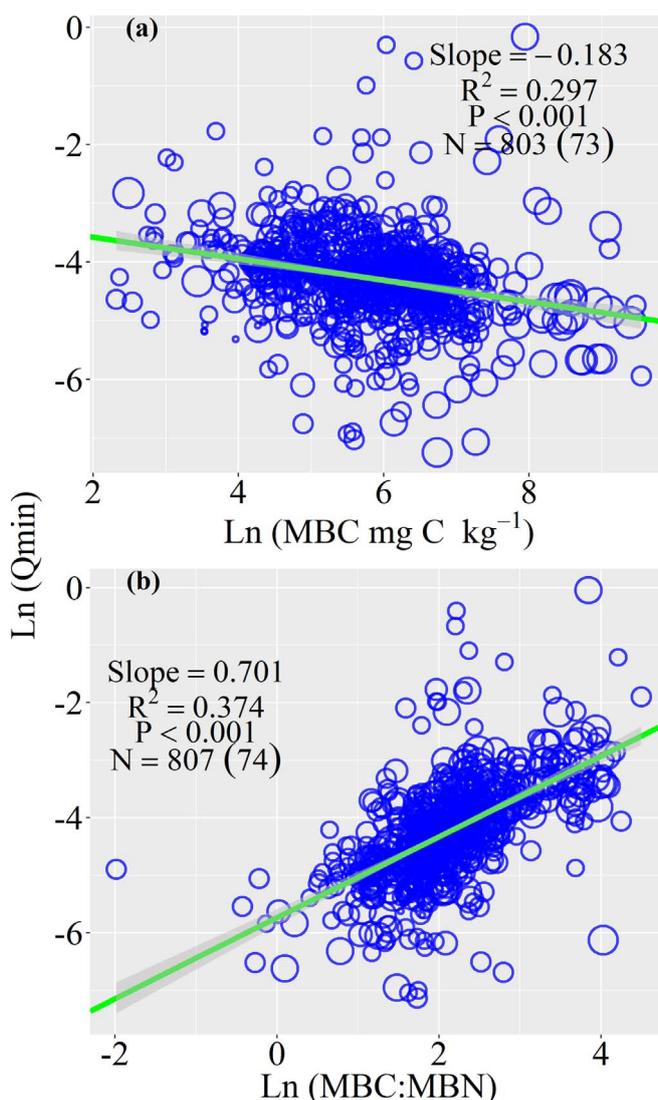


Figure 4. The bivariate relationships between soil metabolic quotient of nitrogen mineralization (Q_{\min}) with the soil microbial biomass carbon (MBC) and the stoichiometry of soil microbial biomass (MBC:MBN) using logarithm transformation data. The green line is the mean slope and grey shades are 95% confidence intervals of the slope by a linear mixed-effect model. The size of blue dots refers to the number of replicates (from 1 to 12). The number after N without parentheses points to observations, and the number in parentheses points to studies.

Q_{\min} decreased with the content of soil organic C with the slope being -0.17 ($r^2 = 0.34$, $P < 0.001$; figure 3(d)) and the content of total soil N ($r^2 = 0.37$, $P = 0.001$; figure 3(e)). Moreover, there was a negative relationship between soil Q_{\min} and the ratio of soil C to N ($r^2 = 0.39$, $P < 0.001$; figure 3(f)). Soil Q_{\min} decreased with soil microbial biomass C ($r^2 = 0.30$, $P < 0.001$; figure 4). But soil Q_{\min} increased with the C:N ratio of soil microbial biomass ($r^2 = 0.37$, $P < 0.001$).

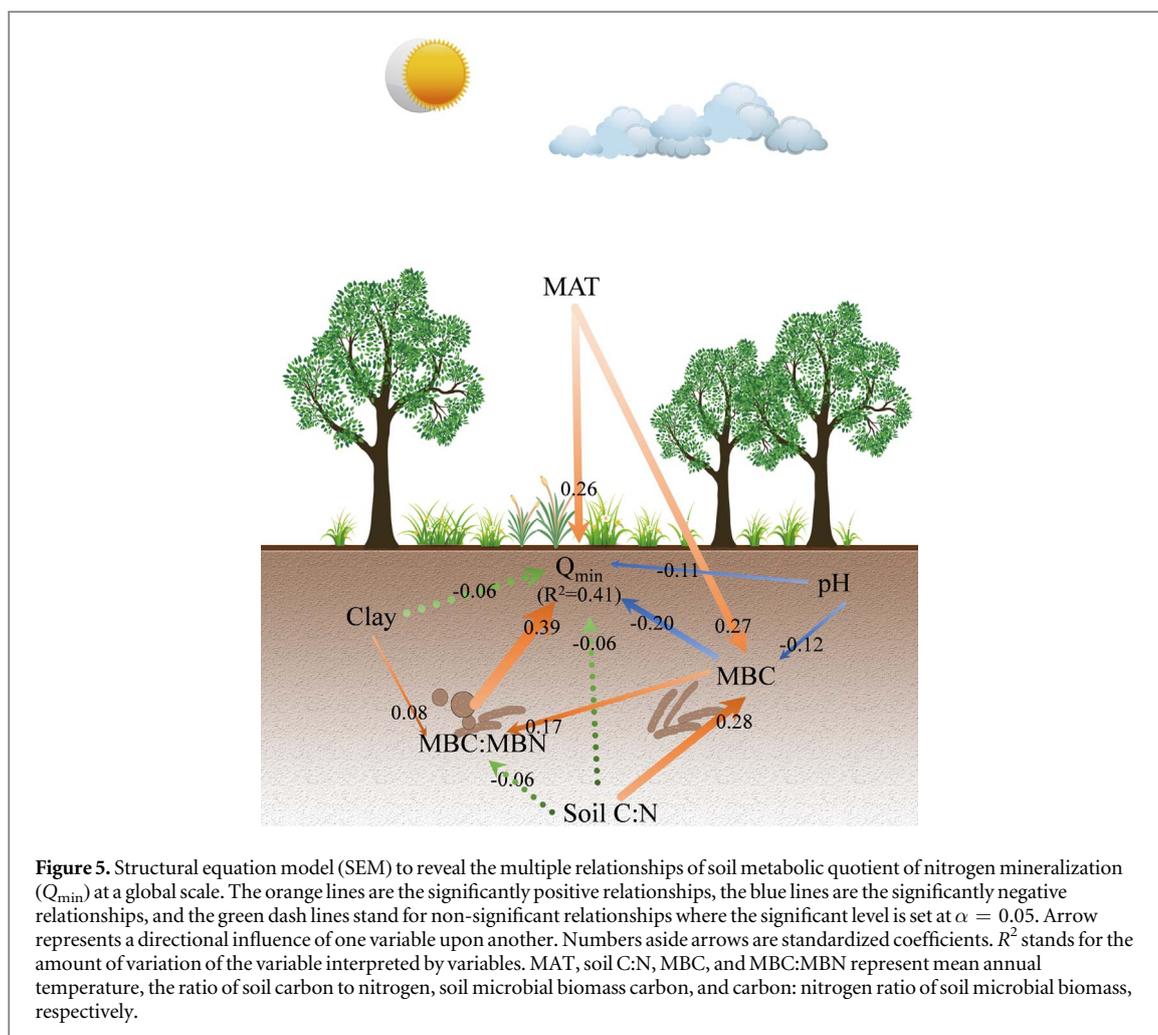
Multivariate relationships between soil Q_{\min} and its controlling factors

SEM indicated that mean annual temperature, soil pH, soil microbial biomass C, the C:N ratio of soil microbial biomass had direct effects on soil Q_{\min} at a global scale (figure 5). Specifically, soil Q_{\min} was positively related to mean annual temperature (coefficient = 0.26, $P < 0.001$) and the C:N ratio of soil

microbial biomass (coefficient = 0.39, $P < 0.001$), while Q_{\min} was negatively related to microbial biomass C (coefficient = -0.20 , $P = 0.024$) and soil pH (coefficient = -0.11 , $P < 0.001$).

Mean annual temperature, soil pH, and the ratio of soil C to N also influenced soil Q_{\min} via changing soil microbial biomass C. The effects from mean annual temperature (coefficient = 0.27, $P = 0.006$) and the ratio of soil C to N (coefficient = 0.28, $P < 0.001$) on soil microbial C were positive, whereas the effect from soil pH on soil microbial biomass C was negative (coefficient = -0.12 , $P = 0.046$). Moreover, soil microbial biomass C (coefficient = 0.17, $P < 0.001$) and the content of soil clay (coefficient = 0.08, $P = 0.041$) positively influenced soil Q_{\min} via changing the C:N ratio of soil microbial biomass.

Among these relationships, the correlation between the C:N ratio of soil microbial biomass and



soil Q_{\min} was prominent with standardized coefficient of 0.39. The total effect (the sum of direct and indirect effects) of mean annual temperature on soil Q_{\min} was of the second importance (standardized coefficient = 0.21). The lesser important factors included soil microbial biomass C (total effect = -0.13) and soil pH (total effect = -0.09).

The bivariate relationships between soil Q_{\min} and impacting factors in different ecosystems

Soil Q_{\min} correlated positively with the C:N ratio of soil microbial biomass in all ecosystem types, with the slope being 0.38 (SE = ± 0.075 ; $P < 0.001$) in croplands, 0.22 (SE = ± 0.061 ; $P < 0.001$) in forests, 0.39 (SE = ± 0.072 ; $P < 0.001$) in grasslands, and 0.50 (SE = ± 0.098 ; $P < 0.001$) in wetlands (figure 6). Besides the C:N ratio of soil microbial biomass, the determinants on soil Q_{\min} differed with ecosystem type. In croplands, soil Q_{\min} correlated positively with mean annual temperature (slope = 0.34, SE = ± 0.191 ; $P = 0.088$) and negatively with soil pH (slope = -0.19 , SE = ± 0.115 ; $P = 0.087$). In forests, soil Q_{\min} correlated significantly with soil microbial biomass C (slope = -0.23 , SE = ± 0.038 ; $P < 0.001$), soil organic C (slope = -0.18 , SE = ± 0.045 ; $P < 0.001$), total soil N (slope = -0.14 ,

SE = ± 0.096 ; $P < 0.001$), and the ratio of soil C to N (slope = -0.22 , SE = ± 0.096 ; $P < 0.001$). In grasslands, soil Q_{\min} was negatively related to soil microbial biomass C (slope = -0.50 , SE = ± 0.094 ; $P < 0.001$), total soil N (slope = -0.25 , SE = ± 0.113 ; $P = 0.030$), and mean annual precipitation (slope = -0.37 , SE = ± 0.155 ; $P = 0.021$). In wetlands, soil Q_{\min} decreased significantly with the mean annual temperature (slope = 0.35, SE = ± 0.141 ; $P = 0.019$).

Discussion

This study reveals the global pattern of soil Q_{\min} and comprehensively quantifies the determinants of soil Q_{\min} . The C:N ratio of soil microbial biomass predominantly determines the variations of soil Q_{\min} at the global scale and in individual ecosystem type in comparison with climate and soil physical and/or chemical properties (figures 5 and 6). This finding, together with the previous one which found that the amount of soil microbial biomass drives the variations of global soil N mineralization (Li *et al* 2019), highlights the roles of soil microbial traits in soil N cycling. Thus, changes in the stoichiometry of soil microbial biomass under climate change and/or anthropogenic

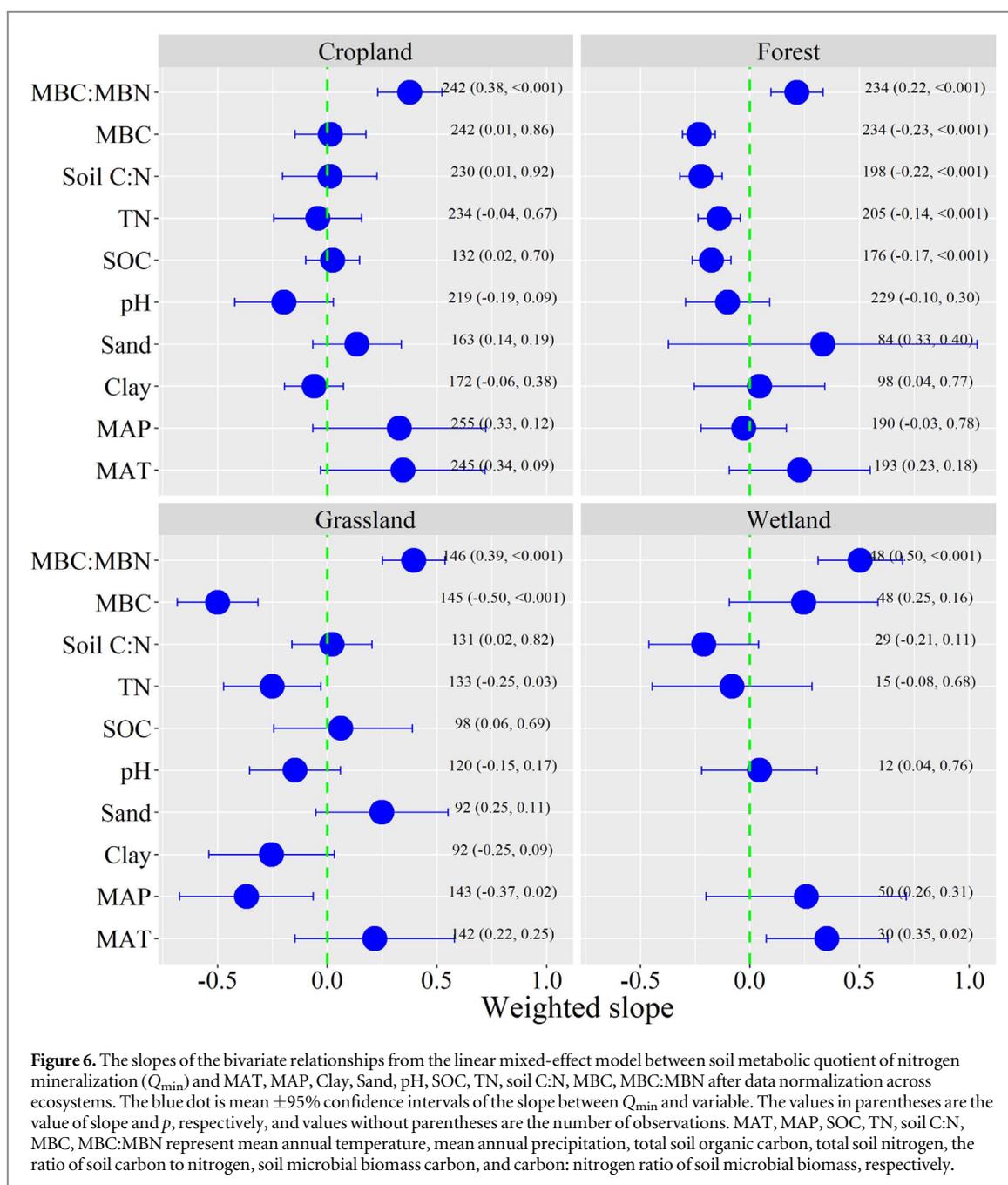


Figure 6. The slopes of the bivariate relationships from the linear mixed-effect model between soil metabolic quotient of nitrogen mineralization (Q_{min}) and MAT, MAP, Clay, Sand, pH, SOC, TN, soil C:N, MBC, MBC:MBN after data normalization across ecosystems. The blue dot is mean \pm 95% confidence intervals of the slope between Q_{min} and variable. The values in parentheses are the value of slope and p , respectively, and values without parentheses are the number of observations. MAT, MAP, SOC, TN, soil C:N, MBC, MBC:MBN represent mean annual temperature, mean annual precipitation, total soil organic carbon, total soil nitrogen, the ratio of soil carbon to nitrogen, soil microbial biomass carbon, and carbon: nitrogen ratio of soil microbial biomass, respectively.

disturbances would cause significant impacts on soil N cycling.

The drivers of global soil Q_{min}

The C:N ratio of soil microbial biomass is the paramount factor determining the global variation of soil Q_{min} , which showed positive relationship with each other. Previous studies found a negative relationship between soil metabolic quotient of soil respiration and microbial C:P, which indicates the significant influences of microbial stoichiometry on soil metabolic quotient of soil respiration (Hartman and Richardson 2013). As pointed out by Cleveland and Liptzin (2007), soil microbial stoichiometry could mirror the relative microbial nutrient limitation. At a global scale, soil microbial biomass is relatively

restricted by N in the terrestrial ecosystem (Cleveland and Liptzin 2007). Therefore, microbes increase N metabolism to gain N. Greater exudation of enzymes used to obtain N from the environment may be a strategy for microbes when available N is limited. Urease is negatively correlated with the contents of soil inorganic N (Ajwa *et al* 1999). Moreover, the arginine deaminase, alanyl aminopeptidase, lysyl-alanyl aminopeptidase increase under low N treatment (Enowshu *et al* 2009). The exudation of enzymes might consume the N of microbial biomass, which, in turn, result in higher C:N ratio of soil microbial biomass. When N is limiting, the metabolism of soil microbes should be more sensitive to N availability. Consistent with our assumption, the catabolic activity of soil microbial biomass increases with the additional N

input in the natural ecosystem (i.e. grassland in Cedar Creek) (Fierer *et al* 2012). In addition, soil physical property (i.e. the content of clay) and microbial biomass influenced soil Q_{\min} via changing the C:N ratio of soil microbial biomass (figure 5), indicating that the properties of soil microbial biomass are the critical bolt for soil Q_{\min} .

Mean annual temperature is the second important controlling factor on soil Q_{\min} on a global scale. The previous experiment also shows that the microbial metabolic quotient of soil respiration substantially increases with temperature (Xu *et al* 2006, Nazaries *et al* 2015). This phenomenon is ascribed to the increasing costs of sustaining microbial activities under higher temperature (Alvarez *et al* 1995), which is verified by decreasing C utilization efficiency under higher temperature (65.4% for 15 °C versus 59.5% for 25 °C) (Steinweg *et al* 2008). Additionally, the activities of soil extracellular enzymes accelerate under higher temperature. For example, the activity of soil urease significantly increases by 33% in a natural forest when the soil temperature rises by 0.55 °C (Xu *et al* 2010). The results from 16 experiments across the United States revealed that experimental warming significantly increases proteolytic activity by 18% in organic horizons (Brzostek *et al* 2012). When the soil temperature is increased by 0.98 °C, soil N-acetylglucosaminidase increases by 5% or even up to 21% (Zhou *et al* 2013). These suggest that increasing mean annual temperature under global climate change might accelerate soil N cycling via motivating soil Q_{\min} .

The size of soil microbial biomass C negatively influenced soil Q_{\min} , which might attribute to three reasons. First, given the same amount of soil substrate, with more soil microbes, the efficiency of decomposing substrate might become less. Second, soil microorganisms are highly diverse, and they could be grouped into active, potentially active, and dormant microbial states (Blagodatskaya and Kuzyakov 2013). In general, majority of soil microbial biomass cannot participate in ecosystem processes (Blagodatskaya and Kuzyakov 2013). This might account for the negative relationship between soil microbial biomass C and Q_{\min} . Third, the bigger soil microbial community might arouse a greater competition with one another. Given the scarcity of resources in most soil ecosystems, more soil microbes might lead to fierce competition (Ghoul and Mitri 2016). The microbes might excrete the secondary metabolites, i.e. antibiotics, to compete with one another. This could consume the energy of microorganism. It was reported that 5%–10% of genomes link to secondary metabolites in actinomycetes (Nett *et al* 2009). Consistent with the negative relationship between soil Q_{\min} and microbial biomass C, soil microbial metabolism of respiration with ecosystem succession shows the contrary trends in comparison with that of the microbial biomass (Wardle and Ghani 2018).

Soil pH is the second negative controller on global soil Q_{\min} . Soil pH could negatively influence the activities of enzymes taking part in N cycling. A global synthesis revealed that β -N-acetylglucosaminidase decreases (slope = -0.54) with pH changing from 4 to 9 (Sinsabaugh *et al* 2008). The activity of urease decreases when soil pH increased from 4.5 to 8.5 (Singh and Nye 1984). In addition, previous studies found that some protease is optimal under acidic conditions (Kamimura and Hayano 2000).

The drivers of soil Q_{\min} in different ecosystems

Although the positive relationships between soil Q_{\min} and C:N ratio of soil microbial biomass were consistently found across all ecosystem types, there were different drivers, other than the C:N ratio of soil microbial biomass, on soil Q_{\min} in different ecosystem types. In forests and grasslands, soil Q_{\min} was correlated negatively with soil microbial biomass C. The soils in forests ($644 \mu\text{g g}^{-1}$ soil) and grasslands ($416 \mu\text{g g}^{-1}$ soil) usually possess more microbial biomass C than adjacent croplands ($313 \mu\text{g g}^{-1}$ soil) (Prasad *et al* 1995). It was reported that soil microbial biomass increases along the forest succession (Wardle and Ghani 2018), the competition among microorganisms likely increases as well, indicating an increasing negative regulation of microbial biomass on Q_{\min} . In grasslands, soil Q_{\min} also significantly correlated with mean annual precipitation. The water shortage in grasslands might limit soil N cycling (Reichmann *et al* 2013, Hu *et al* 2015). In wetlands, soil Q_{\min} significantly accelerated with higher mean annual temperature. The higher temperature can expedite the microbial metabolism (Tveit *et al* 2015) and the activities of soil extracellular enzymes (e.g. urease increased by 9%; (Bai *et al* 2018)). Soil N mineralization generally occurs under aerobic conditions, the anaerobic condition of wetland might partially mask the other relationship between soil Q_{\min} and soil microbial properties (i.e. microbial biomass C).

In croplands, the insignificant relationship between soil Q_{\min} and microbial biomass C may be due to that anthropogenic disturbance significantly impacts soil microbial biomass (Helgason *et al* 2010, Da Silva *et al* 2014). The croplands exposed to greatest anthropogenic disturbances, such as tillage, fertilization, etc, may directly affect the size of soil microbial biomass. For instance, soil microbial biomass C decrease by 19% under tillage (Zuber and Villamil 2016), wherein the relationship between soil Q_{\min} and microbial biomass should be enhanced. However, the disturbance could break the competition among the community (Huston 1979). For example, tillage could weaken the competition within the soil microbial community (Bailey and Lazarovits 2003). Particularly, fertilization (e.g. urea) provide more substrate to mineralize by microbial biomass, so the negative relationship between soil Q_{\min} and microbial biomass

weakened or even disappeared (figure 6). However, soil pH exhibited marginally significantly negative influence on soil Q_{\min} . The fertilization could elicit soil acidification (Guo *et al* 2010). The acidification could positively affect soil Q_{\min} by changing the activities of soil enzymes in N cycling. For instance, soil urease activity decreases with higher soil pH (Singh and Nye 1984).

Implications and uncertainties

The changes in soil microbial stoichiometry under global change will play an important role in soil N cycling via changing soil Q_{\min} . As reported, the ratio of C to N in bacteria averages 6.5, but that in fungi is 5–17 (Cleveland and Liptzin 2007), therefore, any shift in the ratio of fungi to bacteria under global change could eventually change soil Q_{\min} . The results from a 3 year warming experiment showed that the ratio of fungi to bacteria increases 22%–63% (Zhang *et al* 2005). The C:N ratio of soil microbial biomass is also increased by 0.8%–6.2% in an alpine meadow under warming (Fu *et al* 2012). A 70% increase of N mineralization in arctic zones under warming (Aerts *et al* 2006) is partially ascribed to the changes in microbial biomass stoichiometry and increases of enzymatic activities. Additionally, the changes in the stoichiometry of soil microbial biomass, which is significantly decreased under N deposition (Bell *et al* 2010), will negatively affect soil Q_{\min} and subsequently reduce the N mineralization. Moreover, the ratio of fungi to bacteria increases by 8% at elevated CO_2 (Guenet *et al* 2012), which likely results in higher soil Q_{\min} under increasing atmospheric CO_2 concentrations.

More severe soil acidification under N deposition and/or N addition might elicit significant changes in soil N cycling. Apart from the direct effect of soil pH on soil Q_{\min} , the indirect effect via changing the size of soil microbial biomass is also important. Soil pH generally dominates the distribution patterns of bacteria (Fierer and Jackson 2006) and fungi at the global scale (Tedersoo *et al* 2014). The bacterial community is more sensitive to soil pH than fungi (Rousk *et al* 2010). Moreover, the fungal: bacterial growth is significantly decreased with soil pH ranging from 3 to 8 (Rousk *et al* 2011). The meta-analysis showed that soil pH has decreased on average by 0.26 in natural ecosystems (Tian and Niu 2015) and 0.5 in croplands (Guo *et al* 2010). To meet the food demand in the context of population growth, the fertilizer inputs might not decrease in the next century (Erisman *et al* 2008), which will strengthen soil acidification. Eventually, soil acidification would fortify the microbial ability of soil N mineralization.

Current soil N models are built on either the dynamics of N pool (Wang *et al* 2004) or the empirical response of soil mineralization to temperature (Paul *et al* 2002). However, the microbial mechanisms have not been well presented in models to predict soil N

availability. Soil microbial properties, like the size of microbial biomass and the stoichiometry, are very sensitive to environmental changes (Buchkowski *et al* 2015). With mounting data on the stoichiometry of microbial biomass (Xu *et al* 2013), it is urgent to incorporate soil microbial mechanisms into global N cycling model (Wieder *et al* 2015a).

We are aware that changes in soil microbial community and extracellular enzymes are also important for soil N cycling. However, due to data paucity, they are unable to be included in this study. The projection of soil biogeochemical processes will be more precise when the responses of soil microbial communities are taken into consideration (Karhu *et al* 2014). Soil extracellular enzymes are the direct participants in biogeochemical processes, which have drawn growing attentions in biogeochemical processes (Chen *et al* 2018), and there are many enzymes in N cycling, such as urease, proteinase, amidases, and deaminases, *etc*. However, there is a shortage of data to reveal the influences of soil enzymes on soil Q_{\min} on a global scale. In addition, soil Q_{\min} was calculated using the data from laboratory incubation, which might be higher than that calculated using *in situ* data, but they could show a similar relationship at the global scale ($r^2 = 0.87$) (Xu *et al* 2017). The relationships between soil Q_{\min} and the impacting factors remain to be tested when there would be enough data from field studies.

Conclusion

Understanding the drivers of soil Q_{\min} is essential because soil N mineralization and availability are crucial for ecosystem productivity and C sequestration, especially in the context of global climate change or anthropogenic disturbances (Reich and Hobbie 2013, Wieder *et al* 2015b). The present work demonstrates that, although the climate and soil physical and/or chemical properties significantly affect soil Q_{\min} , the stoichiometry of soil microbial biomass primarily determines the variations of soil Q_{\min} at a global scale, and this relationship is consistent across ecosystems. This study is one of the first attempts to quantify the general pattern of Q_{\min} and its dominant drivers across a wide range of climatic and edaphic environments, which moves us toward a more mechanistic understanding of how changes in soil microbial biomass stoichiometry regulate soil N cycling in terrestrial ecosystems. Our findings provide experimental evidence and mechanistic understanding for parameterizing and benchmarking biogeochemical models. We call for future studies on soil microbial traits, with more attention to soil microbial community and extracellular enzymes, to further reveal the biological mechanisms underlying soil Q_{\min} variation.

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Competing interests

The authors declare no competing financial interests.

Author contributions

Z Li and S Niu wrote the first draft. All the authors contributed to the writing of the paper.

Data statement

Any data that support the findings of this study are included within the article. The dataset is archived from published articles. The list of references for dataset is publicly available and can be accessed in the appendix.

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