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## A global synthesis of the rate and temperature sensitivity of soil nitrogen mineralization: latitudinal patterns and mechanisms

## YUAN LIU<sup>1,2</sup>, CHANGHUI WANG<sup>3</sup>, NIANPENG HE<sup>1</sup>, XUEFA WEN<sup>1</sup>, YANG GAO<sup>1</sup>,

SHENGGONG LI<sup>1</sup>, SHULI NIU<sup>1</sup>, KLAUS BUTTERBACH-BAHL<sup>4</sup>, YIQI LUO<sup>5</sup> and GUIRUI YU<sup>1</sup> <sup>1</sup>Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China, <sup>2</sup>University of Chinese Academy of Sciences, Beijing 100049, China, <sup>3</sup>State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China, <sup>4</sup>Institute of Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen 82467, Germany, <sup>5</sup>Department of Microbiology & Plant Biology, University of Oklahoma, Norman, OK 73019, USA

### Abstract

Soil net nitrogen (N) mineralization (N<sub>min</sub>) is a pivotal process in the global N cycle regulating the N availability of plant growth. Understanding the spatial patterns of  $N_{min}$  its temperature sensitivity ( $Q_{10}$ ) and regulatory mechanisms is critical for improving the management of soil nutrients. In this study, we evaluated 379 peer-reviewed scientific papers to explore how  $N_{min}$  and the  $Q_{10}$  of  $N_{min}$  varied among different ecosystems and regions at the global scale. The results showed that N<sub>min</sub> varied significantly among different ecosystems with a global average of 2.41 mg N soil kg<sup>-1</sup> day<sup>-1</sup>. Furthermore, N<sub>min</sub> significantly decreased with increasing latitude and altitude. The  $Q_{10}$  varied significantly among different ecosystems with a global average of 2.21, ranging from the highest found in forest soils (2.43) and the lowest found for grassland soils (1.67) and significantly increased with increasing latitude. Path analyses indicated that N<sub>min</sub> was primarily affected by the content of soil organic carbon (C), soil C:N ratio, and clay content, where  $Q_{10}$  was primarily influenced by the soil C:N ratio and soil pH. Furthermore, the activation energy  $(E_a)$  of soil N mineralization was significantly and negative correlated with the substrate quality index among all ecosystems, indicating the applicability of the carbon quality temperature hypothesis to soil N mineralization at a global scale. These findings provided empirical evidence supporting that soil N availability, under global warming scenarios, is expected to increase stronger in colder regions as compared with that low-latitude regions due to the higher  $Q_{10}$ . This may alleviate the restriction of N supply for increased primary productivity at higher latitudes.

*Keywords:* activation energy, global pattern, mechanism, mineralization, nitrogen availability, substrate quality, temperature sensitivity

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### Introduction

Nitrogen (N) availability is a crucial factor limiting primary productivity in many terrestrial ecosystems (Vitousek & Howarth, 1991; Reich *et al.*, 2006; Elser *et al.*, 2007; Yahdjian *et al.*, 2011) by regulating plant growth and affecting plant species competition (Perakis & Kellogg, 2006; Cole *et al.*, 2008). In most ecosystems, the N availability of plants largely depends on the quantity of soil net N mineralization ( $N_{min}$ ), in which soil organic N is converted to inorganic N by soil

microorganisms and small animals (Chapin et al., 2011). Some studies have demonstrated that N<sub>min</sub> exhibits high spatial and temporal heterogeneity (Knoepp & Swank, 1998), which is regulated by several factors, such as temperature (Guntinas et al., 2012), moisture (Paul et al., 2003), and land-use type (Templer et al., 2005). Given the dynamic global climate changes, with expected increases in global temperature by at least 2 °C by the end of the 21st century (IPCC, 2013), this change in temperature is expected to significantly affect N<sub>min</sub> and soil N availability, which may influence plant growth and primary productivity in terrestrial ecosystems (IPCC, 2013). However, the pattern of  $N_{min}$  at the global scale is unclear, and only a few studies on Nmin have been conducted at the continental scale (Colman & Schimel, 2013; Liu et al., 2016). Determining whether

Correspondence: Nianpeng He and Guirui Yu, tel. +86 10 64889263, fax +86 10 64889399, e-mails: henp@igsnrr.ac.cn (N. H.) and yugr@igsnrr.ac.cn (G. Y.)

Y. Liu and C.H. Wang contributed equally to this work.

the driving factors for  $N_{min}$  are similar at regional and global scales is essential for us understanding of the regulatory mechanisms of  $N_{min}$  and is critical for the estimation of soil N availability in natural or anthropogenic ecosystems.

The temperature sensitivity  $(Q_{10})$  of  $N_{min}$  is commonly defined as the factor by which N<sub>min</sub> increases with a 10 °C rise in temperature (Kirschbaum, 1995). This parameter is important to evaluate the feedback of soil N availability in response to climate warming scenarios (Kirschbaum, 1995; Koch et al., 2007). Individual studies have shown that  $Q_{10}$  varies with vegetation type (Liu et al., 2016), substrate quality (Updegraff et al., 1995; Koch et al., 2007), soil temperature, soil moisture (Kirschbaum, 1995; Sierra, 1997), and soil texture (Zimmermann et al., 2012). In natural ecosystems, these factors are spatially heterogeneous and may result in spatial variations in  $Q_{10}$  values. However, scientists have commonly considered  $Q_{10}$  to be a constant in many models (Manzoni & Porporato, 2009; Wang et al., 2010), leading to high levels of uncertainty in projection of feedback between the terrestrial ecosystem N cycle and climate change. At the regional or global scale, some studies have reported the effects of climatic factors, measurement methods, and vegetation types on the  $Q_{10}$  of soil N mineralization (Peng *et al.*, 2009; Colman & Schimel, 2013; Liu et al., 2016). However, no comprehensive evaluation of the spatial variations of  $Q_{10}$  with geographic variables has been performed to date. Understanding the geographic patterns and regulatory mechanisms of  $Q_{10}$  at a global scale is crucial for better exploring the response of soil N cycling under the scenario of global warming.

As the decomposition of soil organic matter (SOM) is largely affected by substrate quality (Fierer et al., 2005), according to enzyme kinetics, SOM that is more biochemically recalcitrant has a higher  $Q_{10}$  value (Xu *et al.*, 2010). On the basis of the Arrhenius equation, the values of  $Q_{10}$  may increase with increasing activation energy  $(E_a)$  of a chemical reaction (Arrhenius, 1889). Therefore, the enzymatic decomposition of biochemically recalcitrant substrates (higher requirement of  $E_a$ ) should generally be more sensitive to temperature changes than that of more labile substrates (high-quality substrates) (Craine et al., 2010), resulting in an inverse relationship between substrate quality and  $Q_{10}$ , also referred to as the carbon quality temperature (CQT) hypothesis (Fierer et al., 2005; Davidson & Janssens, 2006). Other studies have supported the CQT hypothesis for litter decomposition, soil carbon (C) mineralization in laboratory incubation experiments, and soil respiration in the field (Davidson & Janssens, 2006; Craine et al., 2010; Quan et al., 2014; Wang et al., 2014; Li et al., 2015). Because soil C and N mineralization are closely coupled (Gilmour *et al.*, 1985; Quan *et al.*, 2014), and the substrate quality of C mineralization is positively correlated with the substrate quality of N mineralization (Koch *et al.*, 2007), we assumed that  $N_{min}$ would also be subjected to CQT hypothesis. Because labile substrates [such as dissolved organic carbon (DOC)] gradually decrease with increasing altitude (Gutiérrez-Girón *et al.*, 2015), we assumed that the  $Q_{10}$ values of  $N_{min}$  would increase at higher latitudes worldwide in response to changes in organic substrate quality.

To better understand how  $N_{min}$  and its  $Q_{10}$  vary among different ecosystems and regions at the global scale, a global dataset of  $N_{min}$  in laboratory incubation experiments was collected. Specifically, the main objectives of this study were to analyze the spatial patterns and influencing factors of  $N_{min}$  and its  $Q_{10}$  at global scale and to verify the mechanisms controlling  $Q_{10}$  with respect to soil substrate quality and soil microorganisms.

#### Materials and methods

#### Literature survey and data extraction

Soil net N mineralization (N<sub>min</sub>) is the balance of soil gross N mineralization and soil gross immobilization, which is calculated as the change in NH<sub>4</sub><sup>+</sup>-N plus NO<sub>3</sub><sup>-</sup>-N during incubation and is used to describe soil N availability for plants (Stanford & Smith, 1972). In this study, peer-reviewed papers on N<sub>min</sub> under laboratory incubation experiments were collected from the Web of Science (www.webofknowledge.com) and China National Knowledge Infrastructure (http://epub.cnki.net) from 1980 to 2015. A total of 379 papers describing N<sub>min</sub> and 54 papers describing temperature sensitivity ( $Q_{10}$ ) of N<sub>min</sub> were collected.

The original data of  $N_{min}$  were first extracted from reported tables or graphs using GETDATA GRAPH DIGITIZER software (http://getdata-graph-digitizer.com) or calculated using the change in  $NH_4^+$ -N plus  $NO_3^-$ -N during incubation. At the same time, other auxiliary data, such as geographic information (latitude, longitude, and altitude), climate information (mean annual air temperature [MAT] and mean annual precipitation [MAP]), soil texture (sand, silt, and clay fractions), soil chemical properties (soil pH, soil organic C [SOC], soil total N [TN], soil C:N ratio, soil DOC, soil dissolved organic N, and soil initial inorganic N [ $NO_3^-$ -N and  $NH_4^+$ -N]), and soil microbial properties (microbial biomass C [MBC], microbial biomass N [MBN], and MBC:MBN ratio) were collected from the same literature.

#### Data assembly

To explore the spatial patterns and influencing factors of the potential  $N_{\rm min}$  under optimal conditions, data stemming from optimal laboratory incubation at 20–30 °C and 60–80% field capacity for 2 weeks were used to determine the  $N_{\rm min}$  and

 $Q_{10}$ . Soil mineral N was extracted with 0.05 M K<sub>2</sub>SO<sub>4</sub>. In total, 506 datasets from 379 publications were selected to identify data for N<sub>min</sub> (Appendix S1), and 123 datasets from 54 publications were selected for the analysis of  $Q_{10}$  (Appendix S1).

All sites were classified into different ecosystems according to the dominant vegetation composition (e.g., croplands, grasslands, forests, shrub lands, wetlands, and tundra). Overall, these sites spanned from 46.32°S to 68.63°N in latitude and from 159.5°W to 175.97°E in longitude across the Asian (201 sites), European (108 sites), North American (131 sites), South American (13 sites), African (15 sites), and Oceanian regions (38 sites). These sites covered five major climate zones, that is, tropical, subtropical, temperate, boreal, and subarctic, and included eight biomes, that is, evergreen broad-leaved forests (17 sites), evergreen needle-leaved forests (31 sites), deciduous broad-leaved forests (nine sites), tropical forest (three sites), grasslands (68 sites), croplands (338 sites), shrub lands (21 sites), and wetlands (11 sites), as shown in Fig. 1.

#### Data calculations

 $Q_{10}$  data were selected to reflect the responses of N<sub>min</sub> as the temperature increased by 10 °C and were calculated according to Eqn 1 (Fissore *et al.*, 2013):

$$Q_{10} = (N_2/N_1)^{[10/(T_2 - T_1)]}$$
(1)

where N<sub>1</sub> and N<sub>2</sub> are the soil net N mineralization rate (mg N soil kg<sup>-1</sup> day<sup>-1</sup>) at incubation temperatures  $T_1$  and  $T_2$  (°C), respectively.

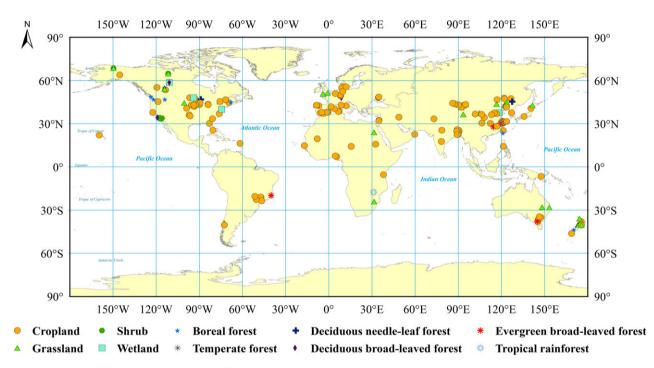


Fig. 1 Distribution of the studying sites in different ecosystems on the global scale.

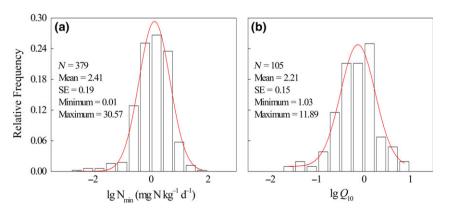


Fig. 2 Frequency distributions of soil net nitrogen mineralization ( $N_{min}$ , a) and temperature sensitivity ( $Q_{10}$ , b) on the global scale.

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To determine whether the CQT hypothesis was applicable to  $N_{min}$  at the global scale, we calculated the activation energy ( $E_a$ ) of  $N_{min}$  according to Eqn 3 (Craine *et al.*, 2010):

$$N = A \times e^{\frac{-E_a}{RT}} \tag{2}$$

$$E_{\rm a} = N \times \ln(Q_{10}) / (\frac{1}{T_1} - \frac{1}{T_2})$$
(3)

where N represents the soil net N mineralization rate (mg N soil kg<sup>-1</sup> day<sup>-1</sup>), *A* is an exponential fit parameter, *R* is the gas constant (8.314 J mol<sup>-1</sup> K<sup>-1</sup>), and  $T_1$  and  $T_2$  are temperatures (K) indicating the 10 °C temperature range for the corresponding  $Q_{10}$ .

The parameter *A* in Eqn 2 was used to represent substrate quality, providing an index of overall substrate quality (availability and lability) of SOM that is catabolized by soil microorganisms at a given point in time (Fierer *et al.*, 2005; Koch *et al.*, 2007).

#### Statistical analysis

The normality of the data was evaluated using the Kolmogorov-Smirnov test, and logarithmic transformation was used to stabilize the distribution to approximate normality when the data did not exhibit normal distribution. Differences in N<sub>min</sub> and Q<sub>10</sub> among different ecosystems and regions were tested using one-way analysis of variance (ANOVA), with least significant differences for multiple comparisons. Regression and correlation analyses were used to determine the associations of climate factors, soil properties, and microbial properties with N<sub>min</sub> and Q<sub>10</sub>. The best-fitted functions were determined using the Akaike information criterion and Bayesian information criterion (Aho et al., 2014). Additionally, path analyses were used to discriminate the direct and indirect factors influencing N<sub>min</sub> and Q<sub>10</sub>. All statistical analyses were conducted using SPSS software (SPSS for Windows, Version 13.0; Chicago, IL, USA). Graphs were drawn using Origin software (Version 8.5; Northampton, MA, USA) and ERSI ArcGIS software (Version 10.1; Redlands, CA, USA). Differences with P values <0.05 were considered significant.

#### Results

#### Spatial patterns and factors influencing N<sub>min</sub>

 $N_{min}$  varied widely on the global scale, ranging from 0.01 to 30.57 mg N soil kg<sup>-1</sup> day<sup>-1</sup>, with an average of 2.41 mg N soil kg<sup>-1</sup> day<sup>-1</sup> (Fig. 2a). Additionally,  $N_{min}$  differed significantly among different regions, ranging from an average of 1.6 mg N soil kg<sup>-1</sup> day<sup>-1</sup> in North America to 2.72 mg N soil kg<sup>-1</sup> day<sup>-1</sup> in Asia (Table 1). Furthermore,  $N_{min}$  differed significantly among ecosystems (P < 0.05), with the lowest observed in soils of shrub ecosystems (0.4 mg N soil kg<sup>-1</sup> day<sup>-1</sup>) and the highest observed in soils of wetland ecosystems (6.1 mg N soil kg<sup>-1</sup> day<sup>-1</sup>; Table 1, Fig. 3a).

	Cropland	рı		Grassland	pu		Forest			Wetland	Ŧ		Shrub			Total			
$N_{min}$	Mean SE		$N^{\ddagger}$	Mean	SE	N	Mean	SE	Ν	Mean	SE	Ν	Mean	SE	Ν	Mean	SE	Ν	P value
North American	1.46	0.16	75	0.99	0.18	15	2.39	0.73	11	7.10	1.90	6	0.40	0.08	21	1.60	0.21	131	0.01
South American	2.14	0.49	8	3.18	I	1	0.78	0.01	4	I	I	None	I	I	None	1.80	0.36	13	0.04
European	2.19	0.26	80	3.25	0.65	12	2.77	0.66	15	2.90	I	1	I	I	None	2.40	0.23	108	0.39
African	2.41	0.68	6	1.15	0.29	4	0.49	Ι	1	Ι	I	None	Ι	Ι	None	1.87	0.46	14	0.35
Asian	2.96	0.34	157	0.82	0.15	20	2.40	0.41	24	0.27	I	1	Ι	Ι	None	2.72	0.28	202	0.23
Oceanian	0.88	0.19	14	2.62	0.45	16	2.49	0.65	8	I	I	None	I	I	None	1.95	0.27	38	0.01
Global	2.59	0.26	343	1.76	0.20	68	2.16	0.27	63	6.10	1.69	11	0.40	0.08	21	2.41	0.19	506	0.01

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Table

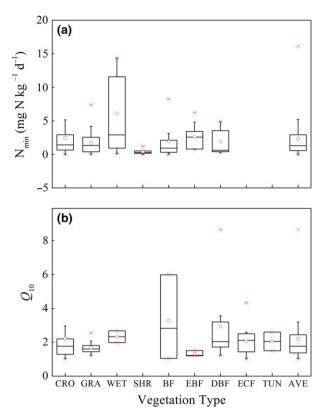
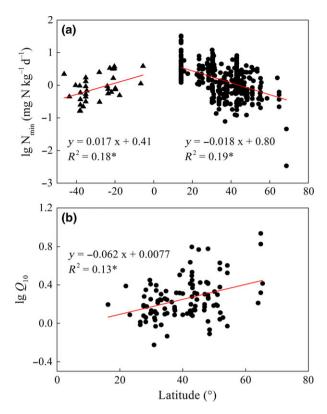


Fig. 3 Changes in soil net nitrogen mineralization ( $N_{min}$ ) and temperature sensitivity ( $Q_{10}$ ) among different ecosystems on the global scale. The boxes show the 25% and 75% percentiles, and the lines and red dots represent the mean and median, respectively. CRO, cropland; GRA, grassland; WET, wetland; SHR, shrub; BF, boreal forest; EBF, evergreen broadleaved forest; DBF, deciduous broadleaved forest; ECF, evergreen coniferous forest; TUN, tundra; AVE, average value.

 $N_{min}$  was negatively correlated with latitude (P < 0.05, Fig. 4a), irrespective of the Northern Hemisphere and Southern Hemisphere. Furthermore,  $N_{min}$  decreased significantly with increasing altitude at the global scale (Fig. S2).

The correlation matrix analysis showed that  $N_{min}$  was significantly influenced by multiple factors (Table 3). Climate (MAT and MAP), soil texture (clay content), soil chemical properties (SOC, TN, and initial  $NH_4^+$ -N concentration), and soil microbial properties (MBC and MBN) were positively correlated with  $N_{min}$ , whereas soil pH, soil C:N ratio, soil MBC:MBN ratio, and soil initial  $NO_3^-$ -N concentration were negatively correlated with  $N_{min}$  (Fig. S5). The results of path analysis indicated that SOC, soil C: N ratio, soil pH, and soil clay fraction were direct factors influencing  $N_{min}$ , together explaining 30% of the variation in  $N_{min}$  (Fig. 6a). MAT and MAP affected the  $N_{min}$  indirectly due to long-term effects on soil physical and



**Fig. 4** Latitude patterns of soil net nitrogen mineralization  $(N_{\min})$  and temperature sensitivity  $(Q_{10})$  with increasing latitude.

chemical properties as well as the microbial community composition.

#### Spatial variations and main factors influencing $Q_{10}$

The  $Q_{10}$  values of N<sub>min</sub> varied from 1.03 to 11.89, with an average of 2.21 (Fig. 2b and Table 2). The mean  $Q_{10}$ was not significantly different among different regions (Table 2). However,  $Q_{10}$  differed significantly among different ecosystems (P < 0.05; Table 2). Soils of forest ecosystems had the highest  $Q_{10}$ , while soils of grassland ecosystems had the lowest  $Q_{10}$  (Fig. 3b and Table 2). Furthermore, the values of  $Q_{10}$  increased significantly with latitude in the Northern Hemisphere (Fig. 4b; such an analysis was not conducted in the Southern Hemisphere due to insufficiency data for  $Q_{10}$ ).

The  $Q_{10}$  values were positively correlated with SOC, soil silt content, and soil C:N ratio, and negatively correlated with soil pH, soil sand content, and initial inorganic N content (Fig. 5 and Table 4). Path analysis indicated that soil pH was the most important direct factor influencing  $Q_{10}$ , accounting for 67% of the variation in  $Q_{10}$  (Fig. 6b). Together, SOC content, soil clay content, soil pH, and soil C:N ratio explained 94% of the variation in  $Q_{10}$  (Fig. 6b).

	Cropla	nd		Grassla	nd	Grassland				Total			
Q <sub>10</sub>	Mean	SE	N†	Mean	SE	Ν	Mean	SE	Ν	Mean	SE	Ν	P value
North American	1.61	0.15	10	2.54	_	1	3.34	0.70	12	2.55	0.40	23	0.038*
South American	2.20	0.77	2	1.57	_	1	2.40	1.17	2	2.15	0.47	5	0.90
European	2.42	0.42	12	1.86	_	1	2.04	0.19	5	2.28	0.28	19	0.58
Asian	1.85	0.26	20	1.60	0.07	13	1.90	0.21	17	1.80	0.12	50	0.63
Oceanian	2.80	0.76	3	_	_	None	_	_	None	2.80	0.76	3	_
Global	2.02	0.16	47	1.67	0.08	16	2.43	0.27	36	2.21	0.16	100	0.12

**Table 2** Changes in the temperature sensitivity  $(Q_{10})$  of N<sub>min</sub> in different ecosystems and regions

†*N* represents the number of study site, – represents none value, the ecosystem type that only has one observation did not involve in the statistical analysis.

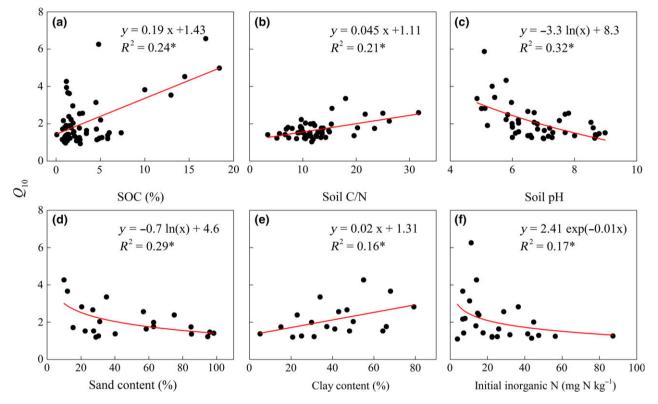


Fig. 5 Relationships between the temperature sensitivity  $(Q_{10})$  of  $N_{min}$  and soil properties.

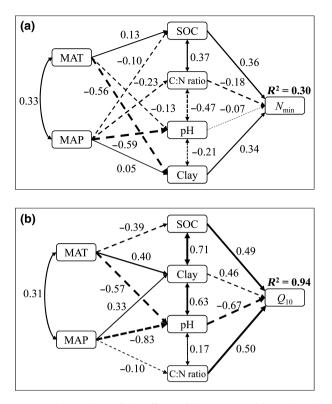
Activation energy ( $E_a$ ) of N<sub>min</sub> was significantly negatively correlated with substrate quality index (A) among cropland, grassland, and forest ecosystems (Fig. 7), indicating that there was a relationship between  $E_a$  and the substrate quality index for most of ecosystems.

#### Discussion

#### Global patterns of soil N<sub>min</sub>

 $N_{min}\xspace$  varied significantly among different ecosystems. The highest value was observed in soils of wetland

ecosystems (average 7.1 mg soil kg<sup>-1</sup> day<sup>-1</sup>), and the lowest occurred in soils of shrubland ecosystems (average 0.4 mg kg<sup>-1</sup> day<sup>-1</sup>). Differences in litter composition and microbial composition were expected to cause differences in N<sub>min</sub> among various ecosystems (Chapin *et al.*, 2011). The lowest N<sub>min</sub> in shrubland ecosystems may be caused by the lower microbial biomass observed in shrubland ecosystems than in other ecosystems (Colman & Schimel, 2013). The *in situ* decomposition of SOM in wetlands was slow due to waterlogging anoxic/acidic conditions, resulting in accumulation of SOM (Bai *et al.*, 2012). When incubated under optimal conditions (optimal temperature and soil



**Fig. 6** Path analysis of the effects of climatic variables and soil properties on the latitude variations of soil net nitrogen mineralization (N<sub>min</sub>) and temperature sensitivity ( $Q_{10}$ ). Solid and dashed arrows represented the positive and negative effects in a fitted structural equation model, respectively. Line thickness indicates the strength of the effects of variables on each other. Models satisfactorily fitted to our data, as suggested by the  $\chi^2$  and RMSEA values [ $\chi^2 = 11.1$  (P = 0.435), RMSEA = 0.021, df = 11 in N<sub>min</sub>; and  $\chi^2 = 6.24$  (P = 0.795), RMSEA = 0, df = 10 in  $Q_{10}$ ).

moisture), without excessive limitation for microbial activity, the  $N_{min}$  is expected to be higher than that in other ecosystems due to the richer SOM. At the global scale,  $N_{min}$  decreased with both latitude and altitude, consistent with a previous study conducted in China (Liu *et al.*, 2016).

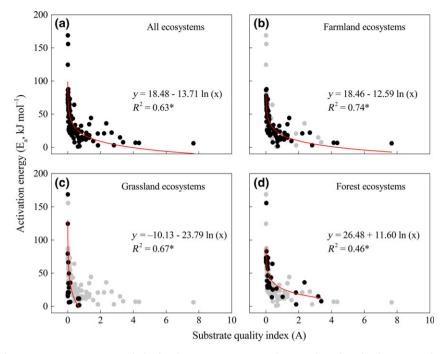
Spatial heterogeneity in climate conditions can lead to dramatic variations in soil properties at the global scale, such as changes in the concentrations of C, N, and P and in soil microbial biomass (Xu *et al.*, 2013). In this study, soil physical and chemical properties as well as microbial biomass exhibited latitudinal patterns (Figs S3 and S4). Moreover, both SOC and soil TN contents have been shown to be higher in soils with a higher clay content (Spain, 1990). Additionally, loam and clay soils always have higher bacteria biomasses than sandy soils (Hassinld *et al.*, 1993). Therefore, the decreased clay content with increasing latitude may reduce microbial biomass, indirectly affecting N<sub>min</sub> (Sollins *et al.*, 1996;

Santruckova et al., 2003). Additionally, soil microbial biomass is a pivotal indicator of global nutrient cycling (Li et al., 2014). Generally, N<sub>min</sub> is positively correlated with MBC and MBN (Hu et al., 2008). Many studies have demonstrated that higher N<sub>min</sub> always correspond to higher soil microbial biomass (Hatch et al., 2000). Furthermore, soil microbial biomass itself is an important pool of readily mineralized organic N in soils (Bonde et al., 1988). In this study, MBC and MBN significantly decreased with both latitude and altitude, mainly due to the low temperatures at higher latitudes and altitudes (Rustad et al., 2001), resulting in a decreased N<sub>min</sub> values with increasing latitude and altitude. Additionally, substrate quality also regulates N<sub>min</sub>. Higher quality compounds always correspond to lower soil C:N ratios and thus are more easily decomposed by microbes (Bengtsson et al., 2003). The C:N ratio of SOM increased significantly with increasing latitude, indirectly explaining the lower Nmin at higher latitudes and altitudes observed in this study.

#### Global patterns of $Q_{10}$ of soil $N_{min}$

The mean  $Q_{10}$  for all ecosystems (2.41) obtained in this study was similar to that estimated for soil C mineralization of global terrestrial ecosystems (Raich & Schlesinger, 1992). Boreal forests have the highest  $Q_{10}$ , indicating that boreal forests should respond more dramatically to predicted increases in temperature, which are supposed to have higher N availability at high latitudes (IPCC, 2013, Xu et al., 2015). This observation may be associated with the geographic conditions, climatic conditions, and vegetation composition of boreal forests. Because boreal forests are mainly distributed in the northern region and are comprised of coniferous or needle vegetation, their litter contains more recalcitrant components than those of other forests, which would increase the energy requirement for microbial decomposition and thus enhance the  $Q_{10}$  values (Xu *et al.*, 2015).

At the global scale, the values of  $Q_{10}$  increased significantly with increasing latitude (increase of 0.0422 per °), indicating that a rise in temperature would dramatically enhance the N<sub>min</sub> at higher latitudes. As described previously (Vanhala *et al.*, 2008),  $Q_{10}$  may be affected by different soil properties, resulting from different climatic conditions and vegetation compositions. Path analysis further showed that  $Q_{10}$  was mainly influenced by SOC content, soil clay content, soil pH, and soil C:N ratio. The labile pool of SOC provides important substrates for microbial metabolism. Therefore, the change in SOC content affects soil microbial activities, causing the temperature response of N<sub>min</sub> to vary among soils with different SOC contents (Zheng *et al.*, 2009). In addition, the composition of the microbial community



**Fig. 7** Relationships between activation energy ( $E_a$ ) of soil net nitrogen mineralization ( $N_{min}$ ) and substrate quality index (A) for different ecosystem types.

Table 3 Correlat	ion coefficients betweeı	ı soil net nitrogeı	n mineralization	(N <sub>min</sub> )	with cl	limatic variab	les and soi	l properties
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	Climatic va	riables	Soil properties						
	MAP	MAT	Sand	Silt	Clay	Soil pH	SOC	Soil C: N ratio	
MAT	0.33*								
Sand	-0.13	0.42*							
Silt	0.34*	-0.068	-0.71*						
Clay	-0.13	$-0.52^{*}$	-0.73*	0.054					
Soil pH	-0.56*	-0.078	0.022	0.044	-0.078				
SOC	-0.051	0.081	-0.083	0.054	0.080	-0.12			
Soil C: N ratio	0.42*	0.023	0.13	-0.071	-0.12	-0.64*	0.34*		
N <sub>min</sub>	0.0064	0.0078	-0.23	-0.050	0.34*	-0.24*	0.44*	-0.29*	

MAT, mean annual air temperature; MAP, mean annual precipitation; SOC, soil organic carbon. \*Significant at P < 0.05 level.

Table 4 Correlation coefficients between the temperature sensitivity  $(Q_{10})$  with climatic variables and soil properties

	Climatic v	ariables	Soil prope	Soil property						
	MAP	MAT	Sand	Silt	Clay	Soil pH	SOC	Soil C:N ratio		
MAT	0.31*									
Sand	-0.62*	$-0.45^{*}$								
Silt	-0.26	-0.068	-0.53*							
Clay	0.59*	0.50*	-0.59*	-0.31						
Soil pH	-0.40*	-0.13	0.74*	-0.15	-0.11					
SOC	-0.27	$-0.54^{*}$	0.74*	$-0.75^{*}$	0.15	-0.45*				
Soil C: N ratio	-0.19	$-0.45^{*}$	-0.15	0.019	-0.31	-0.030	0.79*			
$Q_{10}$	-0.15	0.019	-0.48*	0.46*	-0.25	$-0.55^{*}$	0.49*	0.53*		

MAT, mean annual temperature; MAP, mean annual precipitation; SOC, soil organic carbon.

\*Significant at P < 0.05 level.

is linked with quality and quantity of SOC; thus, the temperature response of  $N_{min}$  decreases with a decrease in SOC (Fierer et al., 2005). Generally, the soil C:N ratio is considered to be a good indicator of soil quality (Sollins et al., 1996). SOM with a higher C:N ratio, for example, derived from litter of boreal forests, is considered a low-quality or recalcitrant substrate. Earlier studies have demonstrated that the activation energy of SOM decomposition (positively related to  $Q_{10}$ ) increases with increasing molecular complexity of the substrate (Bosatta & Agren, 1999). Therefore, the significant increase in the soil C:N ratio with increasing latitude could partially explain the higher  $Q_{10}$  values at higher latitude (Bengtsson et al., 2003). In addition, soil pH significantly affects the  $Q_{10}$  through its effect on the composition and enzyme activity of microbial communities and substrate availability (Priha et al., 2001). Moreover, pH indirectly controls the N<sub>min</sub> by influencing the redox equilibriums of the soil (Kader et al., 2013). Furthermore, the lower  $Q_{10}$  values at lower latitude may result from the long-term adaptation of microorganisms to the increased temperatures in these regions (Santruckova et al., 2003; Barcenas-Moreno et al., 2009).

# *Kinetic theory may explain the global patterns of* $N_{min}$ *and* $Q_{10}$

How SOM decomposition responds to temperature changes may be explained by the kinetic theory of Arrhenius-type reactions (Arrhenius, 1889), wherein the increase in decomposition rate with increasing temperature under substrate availability and enzyme activity is not constrained by the reaction rate. Kinetic theory also suggests that organic compounds with low quality (i.e., those that require a higher  $E_a$ ) should exhibit a higher proportional increase in reaction rate compared with higher quality organic compounds.

The theoretical explanation for the decrease in  $Q_{10}$ with increasing temperature is that as the temperature increases, there is a declining relative increase in the fraction of molecules with sufficient energy to react (Davidson & Janssens, 2006). However, several studies have reported that decomposition rates of low-quality SOM (i.e., recalcitrant substrates) have a higher  $Q_{10}$ compared with those of higher quality and rapidly decomposing compounds (i.e., labile substrates) (Fierer et al., 2005; Davidson & Janssens, 2006; Craine et al., 2010; Erhagen et al., 2013). To date, differences in the temperature responses of labile substrates and recalcitrant substrates have not been clearly clarified (Giardina & Ryan, 2000; Fang et al., 2005). In our study, the  $E_{\rm a}$  of the N<sub>min</sub> and substrate quality index were significantly negatively correlated among forests, grasslands, and croplands at the global scale, which verified that the CQT hypothesis was applicable to soil N mineralization. That is, the enzymatic decomposition of biochemically recalcitrant substrates (higher requirement of  $E_a$ ) should generally be more sensitive to temperature changes than that of more labile substrates (highquality substrates) (Craine *et al.*, 2010). In summary, our study shows that N<sub>min</sub> decreased significantly with increasing latitude at the global scale and the N<sub>min</sub> was more sensitive to temperature changes at higher latitudes. Higher  $Q_{10}$  values at higher latitudes indicated that those regions may have higher N availability for plant growth through higher N<sub>min</sub> rates under global warming scenarios, which may alleviate the restriction of N supply for increased primary productivity at higher latitudes.

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#### References

- Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of AIC and BIC. Ecology, 95, 631–636.
- Arrhenius S (1889) On the rate of reaction of the inversion of sucrose by acids. Journal of Physical Chemistry, 4, 226–248.
- Bai JH, Gao HF, Xiao R, Wang JJ, Huang C (2012) A review of soil nitrogen mineralization as affected by water and salt in coastal wetlands: issues and methods. *Clean-Soil Air Water*, 40, 1099–1105.
- Barcenas-Moreno G, Gomez-Brandon M, Rousk J, Baath E (2009) Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. *Global Change Biology*, 15, 2950–2957.
- Bengtsson G, Bengtson P, Månsson KF (2003) Gross nitrogen mineralization, immobilization, and nitrification rates as a function of soil C/N ratio and microbial activity. Soil Biology and Biochemistry, 35, 143–154.
- Bonde TA, Schnürer J, Rosswall T (1988) Microbial biomass as a fraction of potentially mineralizable nitrogen in soils from long-term field experiments. *Soil Biology and Biochemistry*, 20, 447–452.
- Bosatta E, Agren GI (1999) Soil organic matter quality interpreted thermodynamically. Soil Biology and Biochemistry, 31, 1889–1891.
- Chapin FS III, Chapin MC, Matson PA, Vitousek P (2011) Principles of Terrestrial Ecosystem Ecology, pp. 204–205. Springer Science & Business Media, New York.
- Cole L, Buckland SM, Bardgett RD (2008) Influence of disturbance and nitrogen addition on plant and soil animal diversity in grassland. *Soil Biology and Biochemistry*, 40, 505–514.
- Colman BP, Schimel JP (2013) Drivers of microbial respiration and net N mineralization at the continental scale. Soil Biology and Biochemistry, 60, 65–76.
- Craine JM, Fierer N, Mclauchlan KK (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geoscience*, 3, 854–857.
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.
- Elser JJ, Bracken MES, Cleland EE et al. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, 10, 1135–1142.
- Erhagen B, Oquist M, Sparrman T et al. (2013) Temperature response of litter and soil organic matter decomposition is determined by chemical composition of organic material. *Global Change Biology*, **19**, 3858–3871.
- Fang CM, Smith P, Moncrieff JB, Smith JU (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature*, 433, 57–59.

Fierer N, Craine JM, Mclauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. *Ecology*, 86, 320–326.

- Fissore C, Giardina CP, Kolka RK (2013) Reduced substrate supply limits the temperature response of soil organic carbon decomposition. *Soil Biology and Biochemistry*, 67, 306–311.
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, 404, 858–861.
- Gilmour JT, Clark MD, Sigua GC (1985) Estimating net nitrogen mineralization from carbon dioxide formation. Soil Science Society of America Journal, 49, 1398–1402.
- Guntinas ME, Leiros MC, Trasar-Cepeda C, Gil-Sotres F (2012) Effects of moisture and temperature on net soil nitrogen mineralization: a laboratory study. *European Journal of Soil Biology*, 48, 73–80.
- Gutiérrez-Girón A, Díaz-Pinés E, Rubio A, Gavilán RG (2015) Both altitude and vegetation affect temperature sensitivity of soil organic matter decomposition in Mediterranean high mountain soils. *Geoderma*, 237, 1–8.
- Hassinld J, Bouwman LA, Zwart KB, Bloem J, Brussaard L (1993) Relationships between soil texture, physical protection of organic matter, soil biota, and C and N mineralization in grassland soils. *Geoderma*, 57, 105–128.
- Hatch DJ, Lovell RD, Antil RS, Jarvis SC, Owen PM (2000) Nitrogen mineralization and microbial activity in permanent pastures amended with nitrogen fertilizer or dung. *Biology and Fertility of Soils*, **30**, 288–293.
- Hu C, Cao ZP, Chen YF, Dawson R (2008) Dynamics of soil microbial biomass carbon, mineral nitrogen and nitrogen mineralization in long-term field experiment, Northern China. *Journal of Sustainable Agriculture*, 32, 287–302.
- IPCC (2013) Climate Change 2013:The Physical Scientific Basis. Contribution of Working Group ? to the Fifth Assessment Report of the Intergovernmental. Cambridge University Press, Cambridge and New York, NY.
- Kader MA, Sleutel S, Begum SA, Moslehuddin AZM, De Neve S (2013) Nitrogen mineralization in sub-tropical paddy soils in relation to soil mineralogy, management, pH, carbon, nitrogen and iron contents. *European Journal of Soil Science*, 64, 47–57.
- Kirschbaum MUF (1995) The temperature-dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry, 27, 753–760.
- Knoepp JD, Swank WT (1998) Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. *Plant and Soil*, 204, 235–241.
- Koch O, Tscherko D, Kandeler E (2007) Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils. *Global Biogeochemical Cycles*, 21, 1–11.
- Li P, Yang YH, Han WX, Fang JY (2014) Global patterns of soil microbial nitrogen and phosphorus stoichiometry in forest ecosystems. *Global Ecology and Biogeogra*phy, 23, 979–987.
- Li J, He N, Wei X, Gao Y, Zuo Y (2015) Changes in temperature sensitivity and activation energy of soil organic matter decomposition in different Qinghai-Tibet plateau grasslands. *PLoS ONE*, **10**, e0132795. doi:10.1371/journal.
- Liu Y, He N, Wen X, Yu G, Gao Y, Jia Y (2016) Patterns and regulating mechanisms of soil nitrogen mineralization and temperature sensitivity in Chinese terrestrial ecosystems. Agriculture, Ecosystems and Environment, 215, 40–46.
- Manzoni S, Porporato A (2009) Soil carbon and nitrogen mineralization: theory and models across scales. Soil Biology and Biochemistry, 41, 1355–1379.
- Paul KI, Polglase PJ, O'Connell AM, Carlyle JC, Smethurst PJ, Khanna PK (2003) Defining the relation between soil water content and net nitrogen mineralization. *European Journal of Soil Science*, 54, 39–47.
- Peng SS, Piao SL, Wang T, Sun JY, Shen ZH (2009) Temperature sensitivity of soil respiration in different ecosystems in China. Soil Biology and Biochemistry, 41, 1008–1014.
- Perakis SS, Kellogg CH (2006) Imprint of oaks on nitrogen availability and 815N in California grassland-savanna: a case of enhanced N inputs? *Plant Ecology*, **191**, 209–220.
- Priha O, Grayston SJ, 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, 17–24.
- Quan Q, Wang CH, He NP et al. (2014) Forest type affects the coupled relationships of soil C and N mineralization in the temperate forests of northern China. Scientific Reports, 4, 6584. doi: 10.1038/srep06584.
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, 44, 81–99.
- Reich PB, Hobbie SE, Lee T *et al.* (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO2. *Nature*, **440**, 922–925.
- Rustad LE, Campbell JL, Marion GM et al. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.
- Santruckova H, Bird MI, Kalaschnikov YN *et al.* (2003) Microbial characteristics of soils on a latitudinal transect in Siberia. *Global Change Biology*, **9**, 1106–1117.

- Sierra J (1997) Temperature and soil moisture dependence of N mineralization in intact soil core. Soil Biology & Biochemistry, 29, 1557–1563.
- Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma*, 74, 65–105.
- Spain AV (1990) Influence of environmental conditions and some soil chemical properties on the carbon and nitrogen contents of some tropical Australian rainforest soils. Australian Journal of Soil Research, 28, 825–839.
- Stanford G, Smith S (1972) Nitrogen mineralization potentials of soils. Soil Science Society of America Journal, 36, 465–472.
- Templer PH, Groffman PM, Flecker AS, Power AG (2005) Land use change and soil nutrient transformations in the Los Haitises region of the Dominican Republic. Soil Biology and Biochemistry, 37, 215–225.
- Updegraff K, Pastor J, Bridgham SD, Johnston CA (1995) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecological Applications*, 5, 151–163.
- Vanhala P, Karhu K, Tuomi M, Bjorklof K, Fritze H, Liski J (2008) Temperature sensitivity of soil organic matter decomposition in southern and northern areas of the boreal forest zone. Soil Biology and Biochemistry, 40, 1758–1764.
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, **13**, 87–115.
- Wang YP, Law RM, Pak B (2010) A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences*, 7, 2261–2282.
- Wang Q, Wang D, Wen XF, Yu GR, He NP, Wang RF (2014) Differences in SOM decomposition and temperature sensitivity among soil aggregate size classes in temperate grasslands. *PLoS ONE*, **10**, doi:10.1371/journal.pone.0117033.
- Xu X, Zhou Y, Ruan HH, Luo YQ, Wang JS (2010) Temperature sensitivity increases with soil organic carbon recalcitrance along an elevational gradient in the Wuyi Mountains, China. Soil Biology and Biochemistry, 42, 1811–1815.
- Xu XF, Thornton PE, Post WM (2013) A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography*, 22, 737–749.
- Xu Z, Tang S, Xiong L et al. (2015) Temperature sensitivity of soil respiration in China's forest ecosystems: Patterns and controls. Applied Soil Ecology, 93, 105–110.
- Yahdijan L, Gherardi L, Sala OE (2011) Nitrogen limitation in arid-subhumid ecosystems: a meta-analysis of fertilization studies. Journal of Arid Environments, 75, 675–680.
- Zheng ZM, Yu GR, Fu YL, Wang YS, Sun XM, Wang YH (2009) Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: a trans-China based case study. *Soil Biology and Biochemistry*, 41, 1531–1540.
- Zimmermann M, Leifeld J, Conen F, Bird MI, Meir P (2012) Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity? *Biogeochemistry*, **107**, 423–436.

#### **Supporting Information**

Additional Supporting Information may be found in the online version of this article:

 Table S1. Statistics of basic soil properties for different ecosystems.

- Table S2. Correlation coefficients between soil net nitrogen mineralization  $(N_{\rm min})$  with climatic variables and soil properties.
- **Table S3.** Pearson's correlation coefficients between different environment variables and latitude.
- Fig. S1. Spatial distribution of temperature sensitivity ( $Q_{10}$ ). Fig. S2. Changes in soil properties with increasing latitude in the northern hemisphere.
- Fig. S3. Changes in soil properties with increasing latitude in the southern hemisphere.
- Fig. S4. Changes in soil net N mineralization  $(N_{\rm min})$  with elevation on the global scale.
- Fig. S5. Relationships between soil net N mineralization  $(N_{\rm min})$  and climatic variables and between  $N_{\rm min}$  and soil properties.
- **Appendix S1.** Description of climate and soil parameters at the study sites.