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Regional variation in the temperature sensitivity of soil organic matter decomposition in China's forests and grasslands

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Abstract

How to assess the temperature sensitivity (Q_{10}) of soil organic matter (SOM) decomposition and its regional variation with high accuracy is one of the largest uncertainties in determining the intensity and direction of the global carbon (C) cycle in response to climate change. In this study, we collected a series of soils from 22 forest sites and 30 grassland sites across China to explore regional variation in Q_{10} and its underlying mechanisms. We conducted a novel incubation experiment with periodically changing temperature (5–30 °C), while continuously measuring soil microbial respiration rates. The results showed that Q_{10} varied significantly across different ecosystems, ranging from 1.16 to 3.19 (mean 1.63). Q_{10} was ordered as follows: alpine grasslands (2.01) > temperate grasslands (1.81) > tropical forests (1.59) > temperate forests (1.55) > subtropical forests (1.52). The Q_{10} of grasslands (1.90) was significantly higher than that of forests (1.54). Furthermore, Q_{10} significantly increased with increasing altitude and decreased with increasing longitude. Environmental variables and substrate properties together explained 52% of total variation in Q_{10} across all sites. Overall, pH and soil electrical conductivity primarily explained spatial variation in Q_{10}. The general negative relationships between Q_{10} and substrate quality among all ecosystem types supported the C quality temperature (CQT) hypothesis at a large scale, which indicated that soils with low quality should have higher temperature sensitivity. Furthermore, alpine grasslands, which had the highest Q_{10}, were predicted to be more sensitive to climate change under the scenario of global warming.

Keywords: decomposition, forest, grassland, regional variation, soil organic matter, temperature sensitivity

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Introduction

Soil is the largest carbon (C) pool in terrestrial ecosystems, with the decomposition of soil organic matter (SOM) representing one of the major CO_2 fluxes in the global C cycle (Schlesinger & Andrews, 2000). Global warming is expected to increase atmospheric CO_2 concentrations by accelerating SOM decomposition, resulting in a positive feedback between the global C cycle and climate warming (Jones *et al.*, 2003, IPCC, 2013). The strength and direction of this feedback is largely dependent on the temperature sensitivity (Q_{10}) of SOM decomposition (Jones *et al.*, 2003; Friedlingstein *et al.*, 2006), which represents a major source of uncertainty in model projections of climate change (Friedlingstein *et al.*, 2006). Some studies have attempted to investigate regional variation in SOM decomposition among different soil types and under different climatic conditions (Colman & Schimel, 2013; Craine *et al.*, 2010; Song *et al.*, 2014; Xu *et al.*, 2015a). However, controversy over soil C dynamics remains, due to large spatial heterogeneity and variation in the inherent decomposability of SOM (Schmidt *et al.*, 2011). Thus, it is necessary to quantify the spatial variation and the fundamental drivers of Q_{10} to obtain accurate predictions of the amount of C released through SOM decomposition and, ultimately, the feedback to climate change (Jones *et al.*, 2003; Friedlingstein *et al.*, 2006).

Soil organic matter decomposition is affected by the climate (Schimel *et al.*, 1994; Wang *et al.*, 2013), the initial quality and quantity of SOM (Wild *et al.*, 2014; Holden *et al.*, 2015), and soil microbial characteristics (Fang *et al.*, 2005b; Baumann *et al.*, 2013). However, these factors might interact with each other, making it difficult to discern factors that covary in the process of interest (Colman & Schimel, 2013). Using a large-scale incubation experiment, Colman & Schimel (2013) found that soil microbial biomass was the most important factor explaining the spatial variation of soil microbial

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respiration in North America, while climate and substrate only exerted slight indirect effects through their impacts on microbial biomass. Recently, a study conducted under varying temperatures of 5–25 °C demonstrated that precipitation was the best predictor of soil microbial respiration rates in the alpine steppes of China (Ding *et al*., 2016). In previous decades, the C quality temperature (CQT) hypothesis was proposed to explain the relationship between SOM decomposition and soil substrate quality across different ecosystems. This hypothesis demonstrated that the biochemically recalcitrant C pool is more sensitive to changes in temperature than the labile C pool (Fierer *et al*., 2005; Craine *et al*., 2010). However, different incubation methods and different definitions of the recalcitrant C pool led to a discrepancy in predicting the response of SOM decomposition to climate change (Lloyd & Taylor, 1994; Giardina & Ryan, 2000; Fang *et al*., 2005a; Reichstein *et al*., 2005). Furthermore, large-scale predictions of the C balance requires improved parameter support for SOM decomposition (Jones *et al*., 2003; Friedlingstein *et al*., 2006). However, the presence of differences in experimental methods among different studies makes it difficult to compare the same parameters across different regions. This issue generates great uncertainty in predicting how the soil C cycle of the terrestrial ecosystem feeds back to climate change.

Traditional incubation experiments of SOM decomposition were conducted at several different but constant temperatures and were measured at intervals of days, weeks, or months (Knorr *et al*., 2005; Conant *et al*., 2011). As a result, it was difficult to simulate the common scenarios of periodic and continuous temperature change in the field. First, there is an inherent shortcoming in using constant incubation temperature, because large differences in incubation temperature might result in noticeable differences in substrate depletion and microbial adaption at constant temperature. In turn, these issues influence the accuracy of observed Q_{10}, especially in long-term incubation experiments (Reichstein *et al*., 2000; Conant *et al*., 2008). Second, the lower frequency of measurements was not statistically sufficient to simulate the relationship between SOM decomposition rates and temperature accurately. Within a climate warming scenario, accurate descriptions of these relationships are needed to decrease uncertainty when predicting future SOM dynamics as simulated by Earth system models (Jones *et al*., 2003; Friedlingstein *et al*., 2006).

Forests and grasslands represent the two major types of terrestrial ecosystems that cover 70% of the land's surface, and store 55–75% of soil organic C (SOC) (Bonan, 2008; Yoshitake *et al*., 2014). Therefore, small changes of SOM decomposition rates in forest and grassland ecosystems are expected to cause large uncertainty in predicting how the global C cycle feeds back to climate change. The current study conducted a comprehensive study of 22 forest soils and 30 grassland soils to explore regional variation in Q_{10} and its underlying mechanisms. To accomplish this objective, we conducted a novel incubation experiment with periodically changing temperature (5–30 °C), in parallel to measuring soil microbial respiration rates (R_s) continuously. Specifically, the main objectives of study were to: (1) investigate the regional variation in Q_{10} across different ecosystems; and (2) explore the fundamental drivers of spatial variation in Q_{10} across different ecosystems. We hypothesized that forest and grassland ecosystems have significantly different Q_{10} values, due to large differences in soil properties and soil microbial properties. We also hypothesized that the mechanisms regulating spatial variation in Q_{10} differ across different ecosystems.

Materials and methods

Study area and field sampling

We collected soils from 22 forests in the tropical, subtropical, temperate, and cold-temperate regions of China. We also collected soils from 13 alpine grasslands in the Tibetan Plateau and from 17 temperate grasslands in Inner Mongolia (Fig. 1). Mean annual temperature (MAT) at these sites ranged from −3.67 to 23.15 °C, while mean annual precipitation (MAP) ranged from 472.9 to 2265.8 mm. All of the forest sampling sites were located in well-protected national nature reserves to minimize the effect of anthropogenic disturbance. These sites were also located in areas with relatively homogenous vegetation and soil that were strongly representative of each forest type. Grassland sites in Inner Mongolia were located along the transect extending from Baokang Town in the east to Siziwang Banner in the west (Xu *et al*., 2016). Grassland sites in the Tibetan Plateau were selected from a transect extending from Changdu County to Gaer County (Li *et al*., 2015).

Soil samples were collected between July and August 2013. At each forest and grassland site, four sampling plots (30 × 40 m) were established. Topsoil (0–10 cm) was collected from 15 to 30 random locations within each plot. Subsequently, the soil samples were combined to form a composite sample. Visible roots and litter residues were manually removed from each soil sample. Fresh soil samples were sieved through a 2-mm mesh and divided into two subsamples. Approximately 100 g fresh soil was air-dried to analyze basic properties. The remaining soil from each composite sample (2–3 kg) was stored at 4 °C for the subsequent incubation experiments.

Measurement of soil chemical and microbial properties

In the laboratory, we measured the soil pH and soil electrical conductivity (EC) of air-dried soils in a 1 : 2.5 (*v*/*v*) soil/water

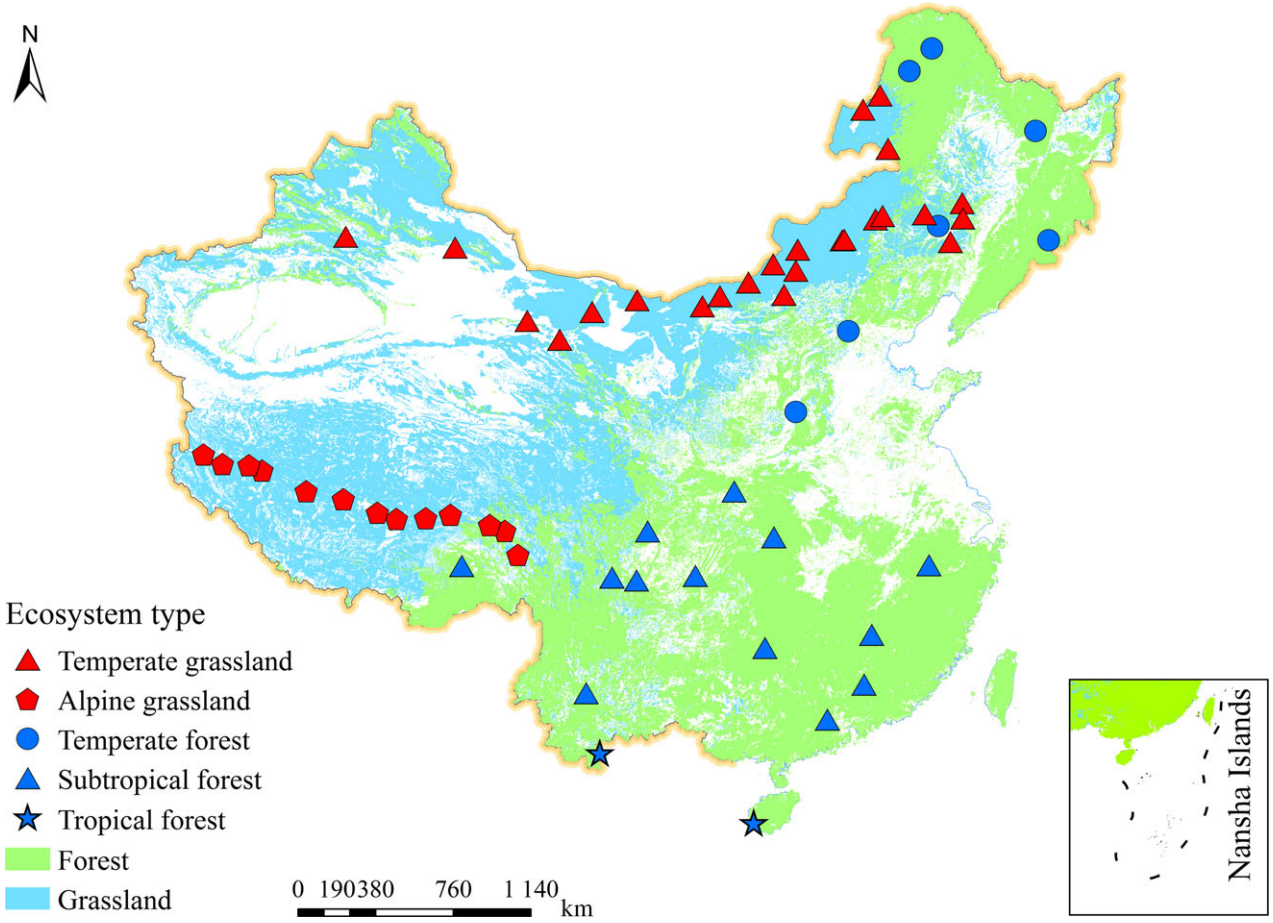

Fig. 1 Spatial distribution of field sampling sites in the forest and grassland ecosystems of China. [Colour figure can be viewed at wileyonlinelibrary.com]

ratio using an Ultrameter-2 pH meter (Myron L. Company, Carlsbad, CA, USA). Soil texture was measured with a Mastersizer-2000 laser particle analyzer (Malvern Company, Worcestershire, England). SOC was analyzed using the H_2SO_4–$K_2Cr_2O_7$ oxidation method (Nelson & Sommers, 1982). Soil total nitrogen concentration (TN) was measured using a modified Kjeldahl wet-digestion procedure (Gallaher *et al.*, 1976), with a 2300 Kjeltec Analyzer Unit (FOSS, Tecator, Höganäs, Sweden). Dissolved organic carbon (DOC) was extracted from incubated soil with distilled water (at a ratio of 1 : 5) and was analyzed with Liqui TOC II (Elementar, Hanau, Germany; Gregorich *et al.*, 2003). After a 2-week incubation period, soil microbial phospholipid fatty acid (PLFA) biomarker analysis was conducted following the method described by Bååth & Anderson (2003) to obtain fungal, bacterial, and actinomycete content (Frostegård *et al.*, 1993; Xu *et al.*, 2015b).

Incubation experiment of SOM decomposition

Soils from all forests and grasslands were used in the incubation experiment. First, the soil samples (20 g, dry weight) were placed in 150-mL polyethylene plastic bottles (four replicates for each soil) and were adjusted to 50% water holding capacity (WHC) by adding deionized water. The methods used to measure WHC are described in He *et al.* (2013). All samples were then pre-incubated at 20 °C for 10 days to activate microorganisms and to minimize the "pulse effect" (Fierer & Schimel, 2002). Plastic bottles were sealed with caps that had small holes for ventilation and to reduce water loss. Water loss was measured and corrected for a weight basis at intervals of 3–4 days. Thereafter, all soil samples were adjusted to 55% WHC and were placed in an incubator with automatic temperature regulation that can gradually increase the temperature from 5 to 30 °C and then decrease it from 30 to 5 °C, within 24-h incubation periods for 14 days (Wang *et al.*, 2016).

Measurement of R_s

R_s was synchronously monitored after 14-day incubation with an automatic sampling and analysis system. A new PRI-8800 Automatic Temperature Control Soil Flux System (PRI-8800; Pre-Eco, Beijing, China) was newly developed and used to measure R_S as a modification of He *et al.* (2013). This system enabled us to continuously vary incubation temperature, in

parallel with measuring R_s at a high frequency (R_s was measured every 75 s) (He *et al.*, 2013; Wang *et al.*, 2016). In brief, an electric water bath controlled by an automatic temperature regulator (Julabo, Seelbach, Ortenau, Germany) was connected to a Li-COR CO_2 analyzer (Li-7100, LI-COR, Lincoln, NE, USA), which records CO_2 concentration every second. The dynamics of R_s over a 24-h period were measured at 20-min intervals for each sample, accompanied by a 12-h warming and 12-h cooling phase. Overall, each sample was measured 72 times during a 24-h cycle. At the same time, soil temperature in plastic bottles was synchronously monitored with a button thermometer (DS 1922L; Maxim Integrated, Dallas, TX, USA). R_s was calculated from the slope of CO_2 concentration and specific transformation factors using Eqn. 1:

$$R_s = \frac{C \times V \times \alpha \times \beta}{m}, \quad (1)$$

where R_s is the rate of soil microbial respiration (μg CO_2–C g^{-1} soil day^{-1}); C is the slope of CO_2 concentration; V is the volume of the incubation bottle and gas tube; m is soil dry weight; α is the transformation coefficient of CO_2 mass; and β is the transformation coefficient of time.

To describe how microbial respiration rates (R_s) are correlated with temperature, we calculated Q_{10} using Eqns (2) and (3):

$$R_s = A.e^{kT}, \quad (2)$$

$$Q_{10} = e^{10k}, \quad (3)$$

where R_s is the rate of soil microbial respiration (μg CO_2–C g^{-1} soil day^{-1}) at a given temperature T (°C) and A and k are the exponential fit parameters. Parameter 'A' represents the basal microbial respiration rate at 0 °C and was used as a simple index of the overall SOM quality that might be utilized by microbes at a specific time point (Mikan *et al.*, 2002; Fierer *et al.*, 2005).

Statistical analyses

Before the analyses, variables that did not meet the assumption of parametric statistical tests (normality and homoscedasticity of errors) were log-transformed. Data normality was tested with a Shapiro–Wilk test. Differences in Q_{10} across different ecosystems were tested using one-way analysis of variance (ANOVA) with LSD test. Regression analysis was used to evaluate the relationships between Q_{10} and soil chemical properties. General linear models (GLMs) were used to evaluate the relative contribution of climatic factors to SOM decomposition across different ecosystems.

Path analysis was used to evaluate the relationships between multiple variables and to determine the direct and indirect factors influencing Q_{10}. Predicted causal relationships between variables were based on prior knowledge of how soil properties affect Q_{10}. By the stepwise removal of nonsignificant paths in the initial model, we selected a final model that best fit our data. The adequacy of the model was determined by the χ^2-test, goodness of fit (GIF) index, and root mean squared error of approximation (RMSEA) index. χ^2 was used to test whether the model reasonably explained the patterns of the data. Favorable model fits were suggested by no significant difference on the χ^2-test ($P > 0.05$), high GIF (>0.9), and low RMSEA (<0.08). Path analysis was conducted in AMOS 18.0 software (IBM, Chicago, IL, USA). Further statistical analyses were conducted in SPSS 13.0 (IBM). A statistical probability of $P < 0.05$ determined significance.

Results

Regional variations in the temperature sensitivity (Q_{10}) of SOM decomposition

Q_{10} is a key parameter used to describe the relationships between the rate of SOM decomposition and changing temperature. Our results showed that Q_{10} varied significantly across different ecosystem types (range: 1.16–3.19; mean: 1.63; CV: 22%; Fig. 2). Q_{10} was ordered: alpine grasslands (2.01) > temperate grasslands (1.81) > tropical forests (1.59) > temperate forests (1.55) > subtropical forests (1.52). Furthermore, the Q_{10} of grasslands (1.90) was significantly higher than that of forests (1.54) ($P < 0.01$; Fig. 3c). However, Q_{10} was not significantly different among tropical, subtropical, and temperate forest soils ($P = 0.51$; Fig. 3a), although Q_{10} was higher in alpine grasslands than in temperate grasslands ($P = 0.059$; Fig. 3b).

Overall, the Q_{10} of forest soils slightly increased with increasing latitude, whereas the Q_{10} of grassland soils decreased with increasing latitude, to some extent (Fig. 4a). Furthermore, Q_{10} significantly declined with increasing longitude in both forest and grassland soils. Q_{10} increased significantly with increasing altitude, whether in forest or grassland ecosystems (Fig. 4b and c).

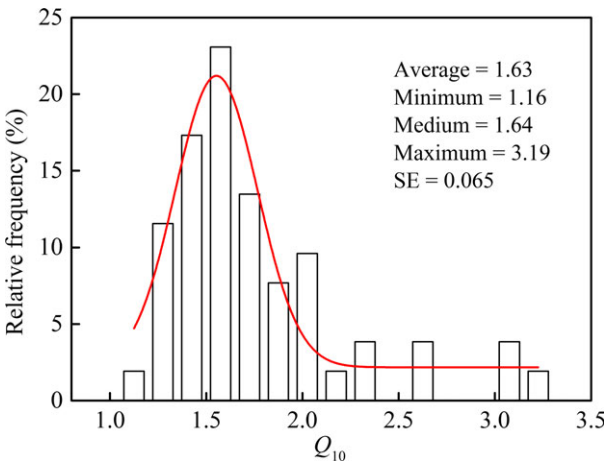

Fig. 2 Frequency distribution in the temperature sensitivity (Q_{10}) of soil organic matter decomposition across forest and grassland sites. [Colour figure can be viewed at wileyonlinelibrary.com]

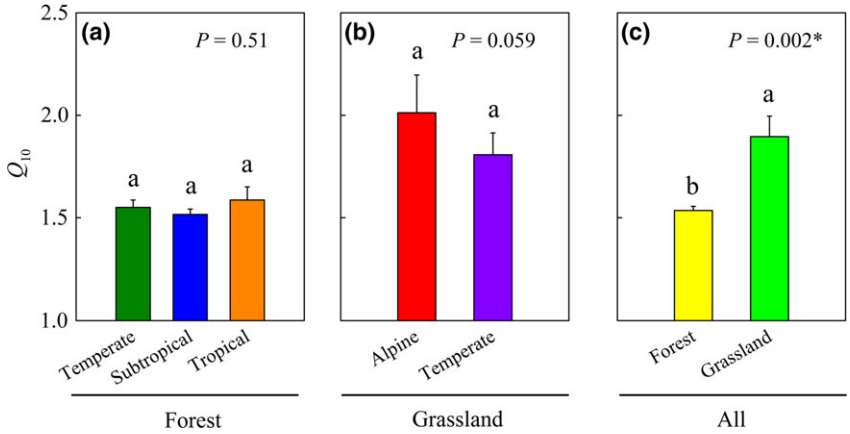

Fig. 3 Regional variation in the temperature sensitivity (Q_{10}) of soil organic matter decomposition across different ecosystem types. Forest (a), grassland (b), whole ecosystem (c). *Data are represented as mean ±1 SD; data with the same letters indicated no significant difference at $P = 0.05$ level. [Colour figure can be viewed at wileyonlinelibrary.com]

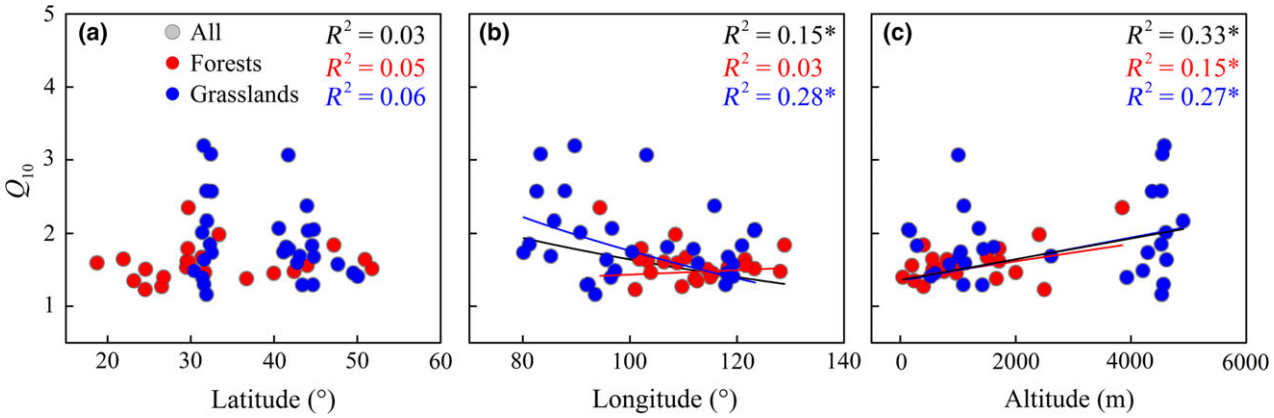

Fig. 4 Spatial patterns in the temperature sensitivity (Q_{10}) of soil organic matter decomposition along latitudinal (a), longitudinal (b), and altitudinal (c) gradients for different ecosystems. *Significant relationship at $P = 0.05$ level. [Colour figure can be viewed at wileyonlinelibrary.com]

Factors influencing spatial variation in Q_{10}

Q_{10} was influenced by a combination of climate (MAT and MAP), soil chemical properties (DOC, soil pH, soil EC), soil nutrients (NH_4^+-N, inorganic-N), and soil microbial properties (fungi, bacteria, and actinomycetes) (Fig. S4). The dominant factors regulating regional variation in Q_{10} differed across different ecosystems. Overall, soil pH had the largest positive prediction for variation in Q_{10} across all ecosystems, followed by the ratio of soil actinomycetes : bacteria (A/B) and soil EC content. In contrast, DOC negatively affected Q_{10} across all ecosystems (Fig. 5). The Q_{10} in forest soils was mainly determined by the soil C : N ratio and soil A/B (Fig. 6a). In comparison, soil actinomycete content and soil A/B strongly regulated the spatial variation of Q_{10} in grassland ecosystems (Fig. 6b). Of note, the dominant factors affecting Q_{10} even differed within the same ecosystem type. For example, in alpine grasslands, soil A/B strongly influenced variation in Q_{10} (Fig. 6c). In contrast, soil EC was the dominant factor influencing the spatial variation of Q_{10} in temperate grasslands (Fig. 6d).

We used the parameter A in Eqn. 2 to represent the overall quality of SOM across different soils. As a result, we found that Q_{10} was significantly negatively correlated with the soil quality index (A) across all ecosystem types (Fig. 7). This finding supports the C quality temperature (CQT) hypothesis, which states that soils with low quality should have higher temperature sensitivity, with SOM decomposition responding to changing temperature, irrespective of ecosystem type.

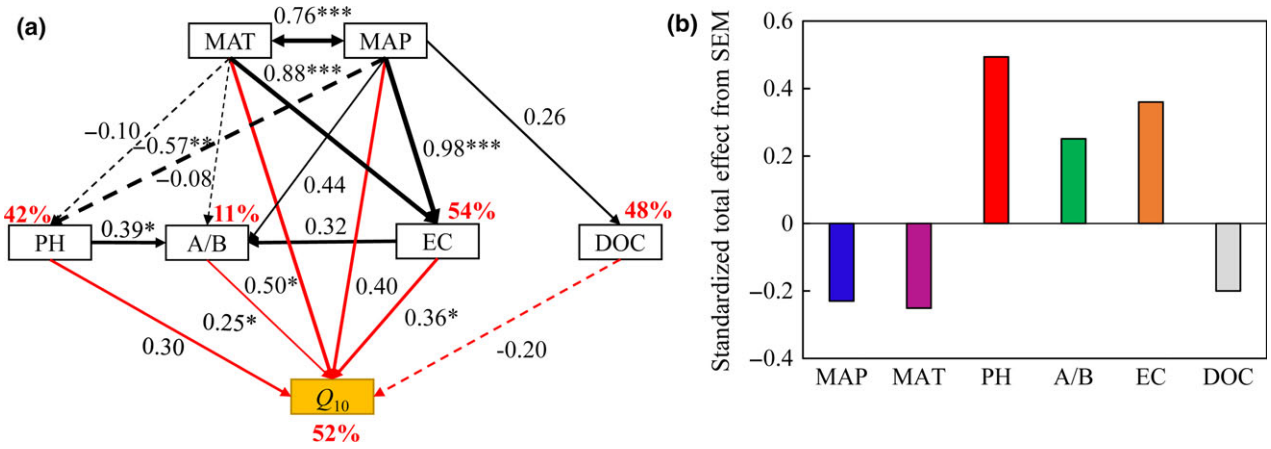

Fig. 5 Path analysis (a) and standardized total effect (b) of climatic variables and soil properties on spatial variation in temperature sensitivity (Q_{10}). Casual influence of MAT and MAP (exogenous variables) on soil actinomycetes : bacteria (A/B), soil pH, soil electrical conductivity (EC), and dissolved carbon (DOC) (endogenous variables). Models satisfactorily fitted to data based on χ^2 and RMSEA analyses [$\chi^2 = 1.15$, df = 4, $P = 0.87$, GFI = 0.99, RMSEA < 0.001). Solid and dashed arrows represent the positive and negative effects in a fitted structural equation model, respectively. Widths of the arrows indicate the strength of the casual relationship. Percentages (R^2) close to endogenous variables indicate the variance explained by climatic and soil factors. *, **, and *** represent a significant relationship at $P = 0.05$, $P = 0.01$, and $P = 0.001$ level, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

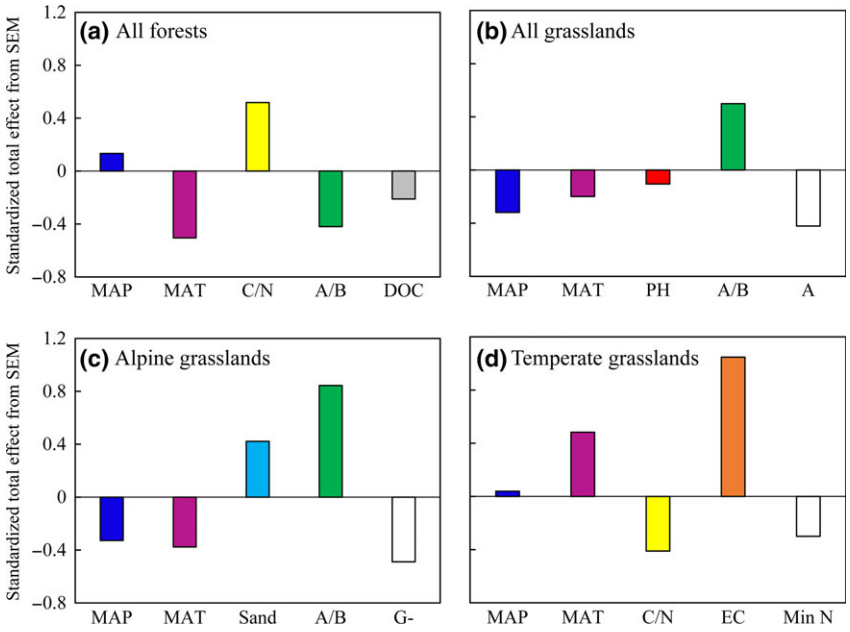

Fig. 6 Standardized total effects of different factors on temperature sensitivity (Q_{10}) across different ecosystems. All forests (a), all grasslands (b), alpine grasslands (c), temperate grasslands (d). Total effects equaled the direct effect plus the indirect effect and were derived from structural equation modeling. MAP, mean annual precipitation; MAT, mean annual temperature; C : N ratio, the ratio of SOC to total nitrogen concentrations; A, actinomycetes; A/B, actinomycete : bacteria ratio; DOC, dissolved organic carbon; EC, electrical conductivity; G–, gram-negative bacteria; Min N, total inorganic nitrogen content. [Colour figure can be viewed at wileyonlinelibrary.com]

Discussion

Regional variation in Q_{10} across different ecosystems

The Q_{10} values of grasslands and forests ranged from 1.16 to 3.19 (mean 1.63), with these values significantly differing within and across ecosystems. The Q_{10} values obtained in our study were comparable to the Q_{10} values measured in the field. For example, Raich & Schlesinger (1992) reported a Q_{10} range of 1.3–3.3 (mean 2.4) for different biomes of the world based on a meta-analysis of *in situ* measurements. Xu *et al.* (2015a)

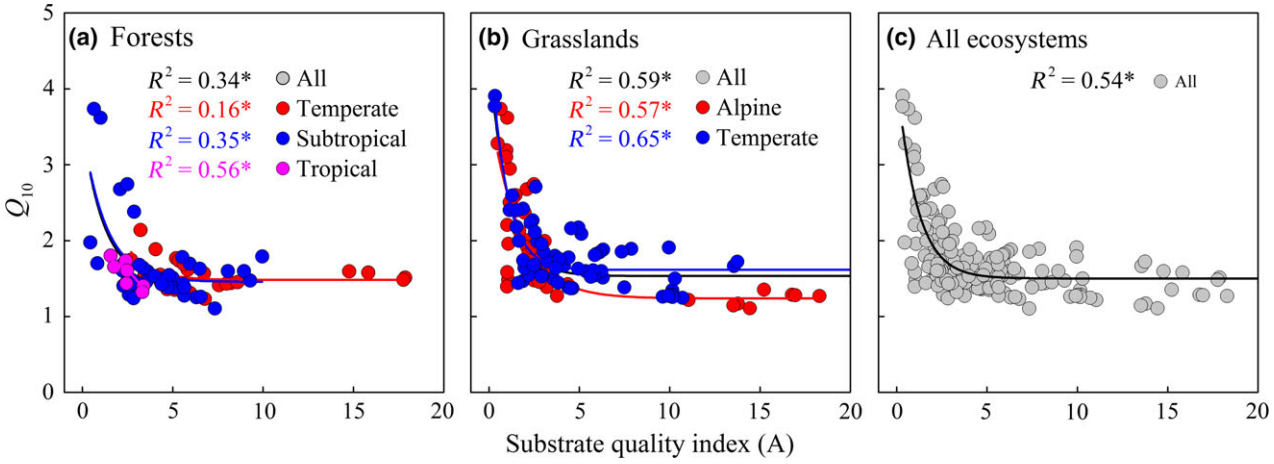

Fig. 7 General negative relationships between temperature sensitivity (Q_{10}) and substrate quality across all ecosystem types. Forests (a), grasslands (b), all ecosystems (c). Fitted function: $Q_{10} = x_0 + a \times \exp(b \times A)$. x_0, a, and b are fitted coefficients. *Significant relationship at $P = 0.05$ level. [Colour figure can be viewed at wileyonlinelibrary.com]

obtained Q_{10} values ranging from 1.10 to 5.18 (mean 2.51) in China's forest ecosystems based on data integration of field observations. Furthermore, in laboratory incubation experiment, Quan *et al.* (2014) reported Q_{10} values ranging from 1.40 to 2.31 among different forest types. Fierer *et al.* (2006) conducted a continental-scale analysis with different constant incubation temperatures and found a large range in Q_{10} values, ranging from 2.2 to 4.6, with an average of 3.0. Our wide range of Q_{10} values combined with other field and laboratory incubation experiments suggests that the use of a single Q_{10} in soil C models could lead to a significant deviations when estimating the sensitivity of soil C dynamics to climate change (Friedlingstein *et al.*, 2006; Zhou *et al.*, 2009).

Spatial patterns in Q_{10} along latitudinal, longitudinal, and altitudinal gradients

Overall, Q_{10} values increased significantly with increasing altitude and decreased with increasing longitude, supporting some previous findings (Gutiérrez-Girón *et al.*, 2015; Xu *et al.*, 2015a). The higher Q_{10} values at higher altitudes and lower longitudes indicated that these regions are more sensitive to climate change. The longitude- and altitude-associated changes in other factors (e.g., MAT, MAP, soil C : N ratio, and soil microbes) were significantly correlated with Q_{10}. MAT and MAP indirectly influenced Q_{10} by affecting soil microbial properties and soil properties (Gutiérrez-Girón *et al.*, 2015). Furthermore, the observed spatial patterns in Q_{10} with altitude and longitude were mainly caused by lower microbial biomass. In contrast, lower soil inorganic nitrogen and higher pH were correlated with increasing altitude and decreasing longitude in this study. However, Q_{10} only slightly increased with increasing latitude in forest ecosystems, whereas it slightly decreased with increasing latitude in grassland ecosystems. These results indicate that high-altitude or low-longitude regions are more sensitive to climate change, due to their relatively higher Q_{10} values.

Factors controlling regional variation in Q_{10}

Overall, soil pH was the dominant factor influencing spatial patterns in Q_{10} at a large scale, followed by soil electrical conductivity (EC), the ratio of soil actinomycetes : bacteria (A : B), and soil dissolved organic carbon (DOC) content. Soil pH significantly affected Q_{10} because it directly influenced the composition of the microbial community and enzyme activity, along with substrate availability (Priha *et al.*, 2001). With increasing soil pH, both the relative abundance and diversity of bacteria and fungi increased (Rousk *et al.*, 2010). The increase in fungi was relatively faster than that of bacteria, resulting in a high fungi : bacteria ratio with increasing pH (Rousk *et al.*, 2010). Fungi are also more likely to decompose recalcitrant SOM, which requires higher activation energy, resulting in an increase in Q_{10} values with increasing soil pH. The ratio of A : B was the dominant factor regulating Q_{10} in alpine grasslands. Actinomycetes are slow-growing gram-positive bacteria that have a filamentous structure similar to that of fungal hyphae (Chapin *et al.*, 2011). The high A : B ratio indicated a high efficiency in decomposing SOM, resulting in a positive relationship between Q_{10} and the ratio of A : B (Table S2).

In addition, soil EC significantly influences Q_{10} by indirectly affecting soil microorganism characteristics and metabolic activity (Xu *et al.*, 2006). Soil microbial

biomass declined significantly with increasing EC, whereas the metabolic quotient (qCO_2) was positively correlated with EC (Iwai *et al*., 2012). Thus, the significant linear relationships between Q_{10} and qCO_2 might explain why Q_{10} increases with increasing EC (Luan *et al*., 2014). DOC is an indicator of easily decomposable substrate. The Michaelis–Menten equation is used to describe the relationship between Q_{10} and soil substrate concentrations (Razavi *et al*., 2015). Michaelis–Menten equation-maximum enzyme activity (V_{max}) and the half-saturation constant (K_m) are temperature sensitive (Davidson & Janssens, 2006). Because both V_{max} and K_m values usually increase with temperature, a canceling effect occurs, which is more pronounced when substrate concentrations are lower than or close to K_m (Gershenson *et al*., 2009). With decreasing DOC content, this canceling effect might be more significant, resulting in Q_{10} declining with decreasing DOC content.

We also found that Q_{10} was significantly affected by soil substrate quality across all ecosystems, based on the negatively exponential relationships between Q_{10} and the substrate quality index (Craine *et al*., 2010). Based on the fundamental principles of enzymes kinetic and the Arrhenius equation, the CQT hypothesis suggests that Q_{10} should increase with increasing activation energy of the reaction (Bosatta & Ågren, 1999; Davidson & Janssens, 2006; Craine *et al*., 2010). Therefore, the decomposition of biogeochemically recalcitrant organic matter (i.e., requiring higher activation energy to degrade) should generally be more sensitive to changes in temperature than the decomposition of more labile organic matter (Craine *et al*., 2010). Furthermore, we found that the soil C : N ratio was the main factor regulating Q_{10} in forest ecosystems. In general, the soil C : N ratio is considered a good indicator of soil quality (Sollins *et al*., 1996). SOM with high C : N ratios being commonly derived from the litter of boreal forests. As a result, this type of SOM is considered a low-quality or recalcitrant substrate. According to CQT hypothesis, recalcitrant substrate characterized with high C : N should have greater Q_{10} than substrates with relatively lower C : N. Overall, the dominant factors regulating Q_{10} across different ecosystems is different. Thus, future models predicting soil C dynamics and C cycle-climate change feedback should account for this variation across different ecosystems.

High sensitivity of grassland ecosystems to temperature change

Soil organic matter decomposition in grassland ecosystems, especially alpine grasslands, was more sensitive than that in forest ecosystems, which was consistent with previous studies (Arevalo *et al*., 2012). Through an incubation experiment, Arevalo *et al*. (2012) showed that the Q_{10} of grasslands (2.13) was significantly higher than that of native aspen forests (1.73). This difference was attributed to the higher C and N content of grasslands than that of aspen forests. In the current study, grasslands had higher Q_{10} than forests because grasslands had higher pH value than forests. Higher pH values are associated with the higher microbial activity of grasslands (Reth *et al*., 2005).

The Q_{10} values in different forest types were not significantly different; however, the Q_{10} of temperate forests was slightly lower than that of tropical forests. In general, deciduous coniferous forests (DCF) tend to be distributed in temperate regions, whereas evergreen broadleaved forests (EBF) tend to be distributed in tropical regions. Previous studies demonstrated that forest type affects the Q_{10} value. For example, the Q_{10} value of DCF was significantly higher than that of EBF, due to the geographic and climatic conditions where vegetation grows (Zheng *et al*., 2009; Xu *et al*., 2015a). The altitude-caused differences in temperature and soil C pools might cause differences in the Q_{10} value between the two forest types (Xu *et al*., 2015a). The Q_{10} value in deciduous forests was significantly higher than that in needle-leafed forests, despite having similar climatic and soil conditions in a mixed forest in Belgium. This difference was due to deciduous forests exhibiting greater seasonal variation in plant growth and phenology than evergreen forests (Curiel Yuste *et al*., 2004).

Furthermore, we found that the alpine grasslands on the Tibetan Plateau were more sensitive to temperature change than the temperate grasslands in Inner Mongolia. Soils with high SOC content are characterized by a capacity to adsorb substantial amount of C compounds onto mineral soil and have low rates of respiration per unit SOC and vice versa (Doetterl *et al*., 2015). The Michaelis–Menten equation indicates that low substrate availability due to physical protection reduces the temperature response of SOC. Therefore, the higher SOC content with low substrate availability in alpine grasslands should cause lower Q_{10} than temperate grasslands with low SOC content and higher substrate availability (Table S1). However, electrical conductivity was the main positive factor affecting Q_{10}; thus, higher electrical conductivity in alpine grasslands might explain why Q_{10} is higher in alpine grasslands than in temperate grasslands (Table S1). In conclusion, soils in alpine grasslands are more vulnerable to climate change under global warming scenarios due to their higher Q_{10} values. Thus, in the future, more studies are required to predict the soil C dynamics and feedback of the soil C cycle to climate change with greater accuracy.

In summary, the temperature sensitivity (Q_{10}) of SOM decomposition varied significantly across

different ecosystems. SOM decomposition in the alpine grasslands of the Tibetan Plateau and higher altitude ecosystems were more sensitive to climate change, due to their higher Q_{10} values. Factors regulating SOM decomposition across different regions were different. Overall, soil pH was the dominant factor regulating regional variation in Q_{10} through an indirect influence on soil microbes. The combination of climate, soil chemical properties, and soil microbial properties explained most of the variations in Q_{10} (55–92%). These findings advance our understanding on regional variation in Q_{10} and how it is likely to be driven by global warming scenarios. Because Q_{10} varied greatly among different ecosystems, future studies focusing on modeling the feedback between the global C cycle and climate change should consider this variation.

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Supporting Information

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

Figure S1. Latitudinal changes of environmental and soil chemical variables.
Figure S2. Longitudinal changes of environmental and soil chemical variables.
Figure S3. Altitudinal changes of environmental and soil chemical variables.
Figure S4. Main factors influencing temperature sensitivity (Q_{10}) across all ecosystems.
Figure S5. Main factors influencing temperature sensitivity (Q_{10}) across all forest ecosystems.
Figure S6. Main factors influencing temperature sensitivity (Q_{10}) in different grasslands.
Figure S7. Path analysis for the effects of climatic variables and soil properties on the spatial variation of temperature sensitivity (Q_{10}) across all sites.
Table S1. Statistical characteristics of soil properties across different ecosystems.
Table S2. Changes in soil microbial properties across different ecosystems.
Table S3. Summary of the general linear models (GLM) for the effects of climate, soil nutrient, soil texture, and soil microbe on temperature sensitivity (Q_{10}).
Table S4. Pearson correlation coefficients between the key parameters of soil organic matter decomposition and soil properties.