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Past climate conditions predict the influence of nitrogen enrichment on the temperature sensitivity of soil respiration

Peng Tian^{1,2,8}, Shengen Liu^{3,8}, Xuechao Zhao^{2,4,8}, Zhaolin Sun^{2,4}, Xiong Yao⁵, Shuli Niu⁶, Thomas W. Crowther⁷ & Qingkui Wang^{1,2}✉

The response of soil carbon release to global warming is largely determined by the temperature sensitivity of soil respiration, yet how this relationship will be affected by increasing atmospheric nitrogen deposition is unclear. Here, we present a global synthesis of 686 observations from 168 field studies to investigate the relationship between nitrogen enrichment and the temperature sensitivity of soil respiration. We find that the temperature sensitivity of total and heterotrophic soil respiration increased with latitude. In addition, for total and autotrophic respiration, the temperature sensitivity responded more strongly to nitrogen enrichment with increasing latitude. Temperature and precipitation during the Last Glacial Maximum were better predictors of how the temperature sensitivity of soil respiration responds to nitrogen enrichment than contemporary climate variables. The tentative legacy effects of paleoclimate variables regulate the response through shaping soil organic carbon and nitrogen content. We suggest that careful consideration of past climate conditions is necessary when projecting soil carbon dynamics under future global change.

¹School of Forestry & Landscape Architecture, Anhui Agricultural University, Hefei 230036, China. ²Huitong Experimental Station of Forest Ecology, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang 110016, China. ³College of Biological and Pharmaceutical Sciences, China Three Gorges University, Yichang 443002, China. ⁴University of Chinese Academy of Sciences, Beijing 100049, China. ⁵College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, China. ⁶Institute of Geographic Sciences and Natural Resource Research, CAS, Beijing 100101, China. ⁷Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 16, 8092 Zurich, Switzerland. ⁸These authors contributed equally: Peng Tian, Shengen Liu, Xuechao Zhao. ✉email: wqkui@163.com

Soil respiration is the second-largest carbon (C) flux from terrestrial ecosystems to the atmosphere, ranging from 68 to 98 Pg C yr⁻¹^{1,2}, and thus plays a vital role in regulating atmospheric CO₂ concentrations. The response of total soil respiration (Rt) to elevated temperature, which is referred to as temperature sensitivity (Q₁₀), regulates the magnitude and direction of global C migration and its feedback to climate change^{3–5}. A growing body of evidence suggests that terrestrial C dynamics are severely affected by atmospheric nitrogen (N) deposition^{6–8}, which has introduced a great amount of reactive N into the terrestrial system and is predicted to persist in the long term⁹. In addition, evidence to support such broad-scale feedback is only correlative rather than causative, so multiple lines of evidence are needed. Yet, how Q₁₀ responds to elevated N deposition at the global scale remains a key knowledge gap that limits predictions of future soil organic carbon (SOC) dynamics and climate change through climate-C cycle models.

The response of Q₁₀ to N enrichment has been widely investigated at individual sites (e.g., ref. 6,7,10,11), with increases and decreases in the Q₁₀ values observed across various N deposition experiments. The considerable variations in the impacts of N enrichment are likely to associate with the large heterogeneity in climates, soil characteristics, and vegetation types in individual studies. For example, the significant roles of bioclimate variables and specific microbial community in regulating N deposition effect on Q₁₀, as well as the comparison of N deposition effects between forest and grassland ecosystems at a regional scale were revealed recently¹². These previous studies have advanced our understanding of the mechanisms underlying the N-enrichment effect on Q₁₀. However, until now, we lack a unified understanding to predict the direction and magnitude of the effects across different regions, limiting our capacity to depict the global pattern of Q₁₀ in response to N enrichment across time and space. Importantly, Rt consists of heterotrophic (Rh) and autotrophic (Ra) components. Ra is derived from roots and the associated rhizosphere, while Rh is essentially the microbial decomposition of litter and soil organic matter. The Q₁₀ values of these components may exhibit different responses to N enrichment, as they are controlled by different mechanisms^{6,13}, which further increases the difficulty in assessing the role of Rt in global C cycling under global climate change. Therefore, understanding how Q₁₀ of Rt and its components respond to N enrichment at the global scale would improve our capacity to predict the responses of soil C dynamics and their feedback to global warming¹.

Mounting evidence suggests that geographical variations in Q₁₀ are primarily driven by climate predictors, particularly the mean annual temperature (MAT) and mean annual precipitation (MAP)^{14–17}. For example, the Q₁₀ values of Rt and Rh were detected to decrease from cold and dry biomes to warm and wet biomes^{14,15,17}, in contrast, increase of Q₁₀ was also found to positively correlate with MAT at a global scale¹⁶. Recently, multiple studies found that the paleoclimate from the Last Glacial Maximum (i.e., approximately 22,000 years ago) could explain a larger amount of the variation in the spatial distribution of the SOC content and microbial diversity than the contemporary climate, being more predictive than the contemporary climate^{18–22}. Until now, however, the link between the paleoclimate and geographical variations in Q₁₀ has not been successfully established, especially under N enrichment conditions. Projections into the future are conditional on the past. On one hand, the direct impact of paleoclimate on soil microbial and plant communities had occurred in the past (for example, in response to an extreme climatic period)^{18,23}, and the consequences of this impact might still be detectable today, directly influencing the C dynamics of microorganism and plant in response to global

change. On the other hand, most soils are polygenetic, that is, archival products of pedogenic processes vary widely over time²⁴. The physiochemical characteristics of the soil, such as pH, SOC, and nutrient contents, have developed slowly under the influence of past climates across millennial time scales^{25,26}. Therefore, the paleoclimate is expected to be potentially associated with the response of Q₁₀ of Rt and its components to N enrichment directly and/or indirectly via the regulations on soil C dynamics and soil properties^{27–29}. It is widely demonstrated that N enrichment impacts the Q₁₀ of soil respiration^{6,7,11}, but whether the global-scale effects of N enrichment on the Q₁₀ are associated with paleoclimate needs to be validated in empirical research. Furthermore, the relative importance of the legacy impacts of the paleoclimate and contemporary climate on the N-enrichment effects on Q₁₀ needs to be examined to enhance our understanding of soil C cycle-climate change feedbacks under global environmental change³⁰.

Here, we synthesized the data collected from 168 published papers based on field N enrichment experiments. The global patterns of the Q₁₀ responses of Rt, Ra, and Rh to N enrichment were investigated to reveal their underlying mechanisms by analyzing the correlations of the effects of N on Q₁₀ with climatic and edaphic factors. In this study, we addressed the following questions: (1) How does N enrichment affect the Q₁₀ of Rt and its components at the global scale? (2) Whether the paleoclimate could predict the N-enrichment effects on Q₁₀ better than the contemporary climate? (3) How does the paleoclimate directly and indirectly regulate the effects of N enrichment on the Q₁₀ of Rt and its components?

Results

Global patterns of Q₁₀ values and their response to N enrichment. Across all observations, the Q₁₀ values of Rt and Rh were positively related to latitude (Fig. 1a, b), but no apparent correlation was found between the Q₁₀ of Ra and latitude (Fig. 1c). The responses of the Q₁₀ values of Rt and Ra to N enrichment expressed positive linear correlations with latitude (Fig. 1a, c), while the response of the Q₁₀ values of Rh to N enrichment was not related to latitude (Fig. 1b). Nitrogen enrichment enhanced the Q₁₀ of Ra on average by 10.6% ($p < 0.05$; Fig. 2c), which was applied to both inorganic (NH₄NO₃) and organic (urea) N applications. In contrast, only NH₄NO₃ significantly increased the Q₁₀ of Rt ($p < 0.05$; Fig. 2a). A low rate of N application increased the Q₁₀ of Rh by 9.0% relative to the control treatment ($p < 0.05$; Fig. 2b). The Q₁₀ of Rt in wetlands and that of Ra in croplands were higher under N enrichment ($p < 0.05$; Fig. 2a, c). The effect sizes of the N-enrichment on Q₁₀ were almost the same in acidic and alkaline soils, although the response of the Q₁₀ of Ra under N enrichment was significant in acidic rather than alkaline soils ($p < 0.05$; Fig. 2c). The methods used for the measurement of Rt and climate zones had limited effect on the responses of Q₁₀ to N enrichment, with slightly positive effects of N enrichment on the Q₁₀ of Ra in temperate zones (Supp. Fig. 3).

Mechanisms underlying the variation in Q₁₀ in response to N enrichment. The variation partitioning results showed that N enrichment could explain the largest unique fraction of the variations in Q₁₀ and the N-enrichment effects on Q₁₀ at the global scale, with an exception of the variations in the N-enrichment effects on Q₁₀ of Ra, in which the variations were explained most by paleoclimate (Fig. 3). In comparison with the contemporary climate, the paleoclimate from the Last Glacial Maximum (about 22,000 years ago) predicted a larger amount of unique fraction of the variations in the N-enrichment effects on the Q₁₀ of Rt (4.90% versus 0.81%), Rh (2.67% versus 1.19%) and Ra (8.97% versus

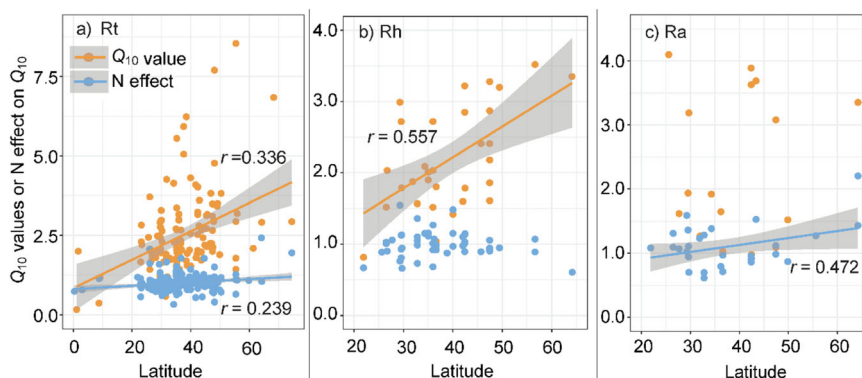


Fig. 1 Geographical pattern of the temperature sensitivity of soil respiration and their responses to nitrogen enrichment. Latitudinal distribution of the temperature sensitivity of total soil respiration (a), heterotrophic respiration (b), and autotrophic respiration (c), and their responses to nitrogen enrichment. The solid black line represents the fitted regression line, and the gray shading represents their 95% confidence band. All relationships showed are significant at a level of 0.01.

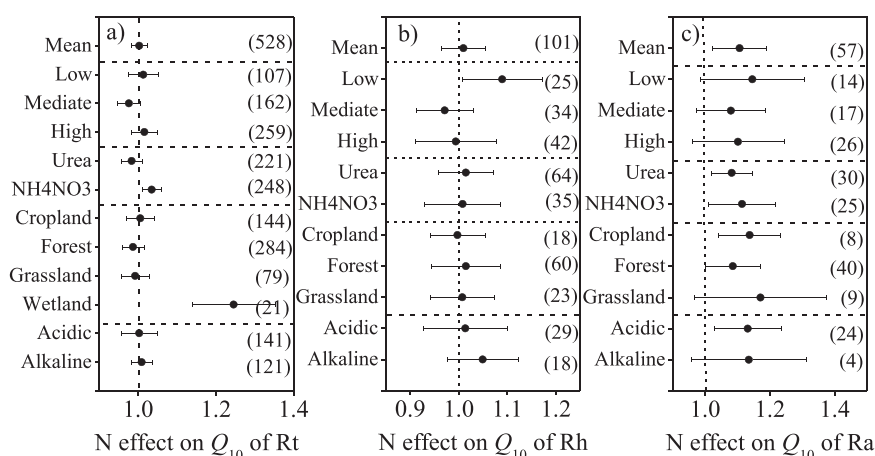


Fig. 2 Influence of nitrogen enrichment on the temperature sensitivity of soil respiration. Overall effect of nitrogen enrichment and the effects of nitrogen form and application rate and ecosystem types on the temperature sensitivity of total soil respiration (a), heterotrophic respiration (b), and autotrophic respiration (c) across all observation. Error bars represent 95% confidence intervals (CIs). The numbers in the brackets represent sample sizes. Significant responses ($p < 0.05$) are recognized if the 95% CIs does not overlap with zero. Vertical dashed lines are the reference of the nitrogen effect of 1.0.

null) (Fig. 3d–f). For the paleoclimate, the best predictors of the global spatial variations in the Q_{10} values of Rt and its components as well as their responses to N enrichment differed (Supp. Tables 2–7). Temperature from paleoclimate, as indicated by mean diurnal range (MDR), mean temperature of coldest quarter (MTCQ), minimum temperature of the coldest month (MinTCM), and temperature annual range (TAR), well predicted the spatial variations in the N effects on the Q_{10} of Rh other than those on the Q_{10} of Ra (Fig. 4 and Supp. Table 7). In contrast, indices of precipitation from paleoclimate, such as annual precipitation (AP), precipitation of wettest month (PWM), and precipitation of driest quarter (PDQ), were consistently good predictors of the spatial variations in the N-enrichment effects on the Q_{10} of Rt (Supp. Table 5) and its components, with the explanations being greatest for the N effects on the Q_{10} of Ra (Fig. 5 and Supp. Table 6).

PiecewiseSEM was performed to further uncover the direct and indirect pathways by which regulatory factors impacted the global-scale variations in the N effects on Q_{10} . Geographical location, climate variables, soil properties, ecosystem types and N application rate collectively explained a large proportion of the global variation in the N effects on the Q_{10} of Rt (56%), Rh (65%), and Ra (56%) when considering the random effects of “sampling

site” (Fig. 6). Apart from the N application rate, climate predictors, including paleoclimate and contemporary climate, consistently exerted great significance in regulating the responses of Q_{10} to N enrichment directly and indirectly by shifting the SOC and total N contents. Among climatic factors, PDQ (precipitation of driest quarter) and PCQ (precipitation of coldest quarter) versus AP (annual precipitation), which are the associated precipitation predictors from paleoclimate, were the most important predictors of the Q_{10} of Rt and Ra in response to N enrichment, respectively (Fig. 6a, c), while the MDR (mean diurnal range) and PS (precipitation seasonality) from paleoclimate exerted great effects on the responses of the Q_{10} of Rh to N enrichment, with MDR being the most significant (Fig. 6b). Furthermore, the global-scale effects of N enrichment on the Q_{10} of Rt and its components were closely associated with ecosystem type, which additionally derived indirect impacts on the N-enrichment effect on the Q_{10} of Rh by altering soil properties (Fig. 6).

Discussion

Our results based on a synthesis of field data provide valuable insights into the latitudinal patterns of the Q_{10} of different Rt components and their responses to N enrichment. In comparison

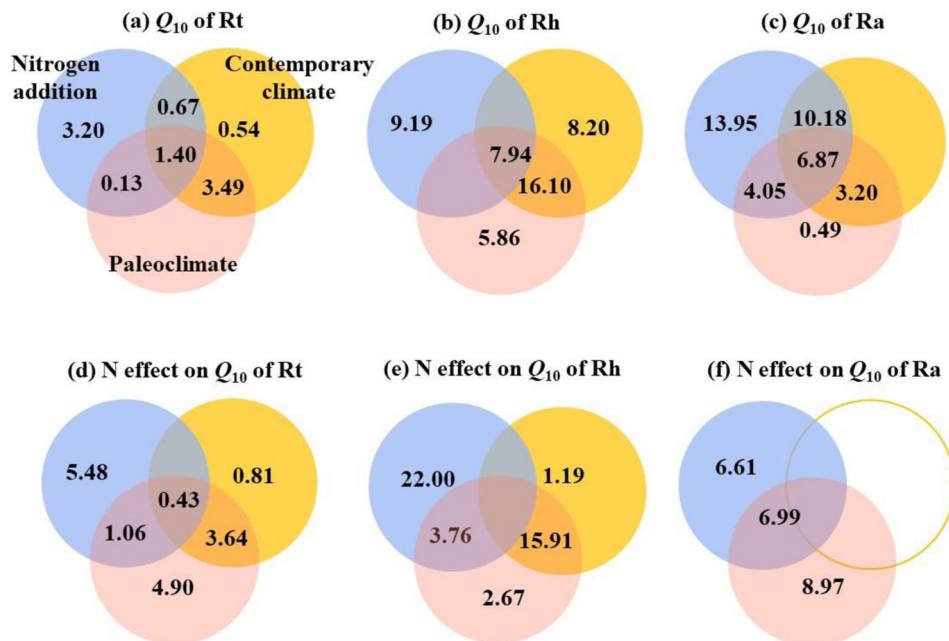


Fig. 3 Environmental and anthropogenic controls on the temperature sensitivity of soil respiration and their responses to nitrogen enrichment.

Variance partitioning for three categories: nitrogen addition traits, contemporary climate, and paleoclimate in explaining variations in the temperature sensitivity of total soil respiration (a), heterotrophic respiration (b), and autotrophic respiration (c) and their responses to nitrogen enrichment (d, e, f), respectively. The blue, yellow, and pink colors represent, respectively, nitrogen addition traits, contemporary climate, and paleoclimate. Values < 0 are not shown. The dotted circle indicates that no predictor was found to be significant in this modeling. See *p* values associated with each ecological predictor in Supp. Tables 2–7.

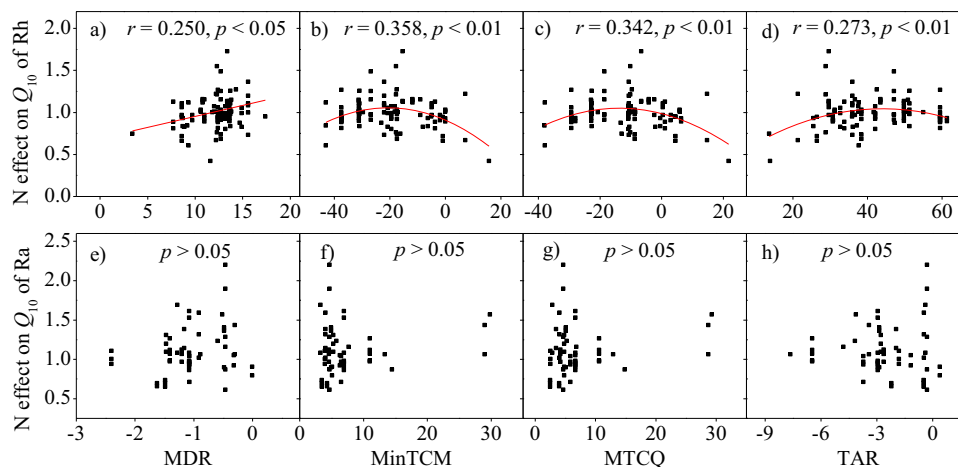


Fig. 4 Dependence of the influence of nitrogen enrichment on the temperature sensitivity of soil respiration on past thermal conditions. The relationships between indices of temperature from paleoclimate and the nitrogen effects on the temperature sensitivity of soil heterotrophic (a–d) and autotrophic respiration (e–h) across all ecosystems. MDR, MinTCM, MTCQ, and TAR denote mean diurnal range, minimum temperature of coldest month, mean temperature of coldest quarter and temperature annual range, respectively. Results of linear mixed effect model are seen in Supp. Table 9.

with previous studies that explored the spatial variations in the Q_{10} of R_t at regional and larger scales (e.g., ref. 7,31–33), our study revealed a consistent global pattern of the in situ Q_{10} of R_t and R_h that linearly increased with latitude (Fig. 1a, b); however, this pattern was not revealed for R_a (Fig. 1c). This finding indicates that the latitudinal distributions of the Q_{10} of R_a and R_h were different and that the spatial variations in the Q_{10} of R_t were mainly contributed by Q_{10} of R_h . Moreover, the lack of apparent correlation between the Q_{10} of R_a and latitude might be partly attributed to the indirect measurement of R_a via separating R_h from R_t , which could introduce great variation in R_a . Strikingly, the sensitivities of R_t and R_h to global warming were greater in

high-latitude ecosystems than in low-latitude ecosystems, which was in line with previous observations that Q_{10} of R_t in colder regions was higher than that in warmer regions^{14,33}. This spatial pattern was also supported by the negative correlation of Q_{10} values with the MAT from contemporary climate (Supp. Fig. 2), suggesting that the sensitivity of R_t and its heterotrophic component to elevated temperature may potentially decline under global warming^{1,34}.

The changes in the latitudinal patterns of the Q_{10} values of R_h and R_a caused by N enrichment (Fig. 1b, c) were evidenced across our study sites. Our study first clarified the inconsistent spatial patterns of the N-enrichment effects on the Q_{10} values of R_h and

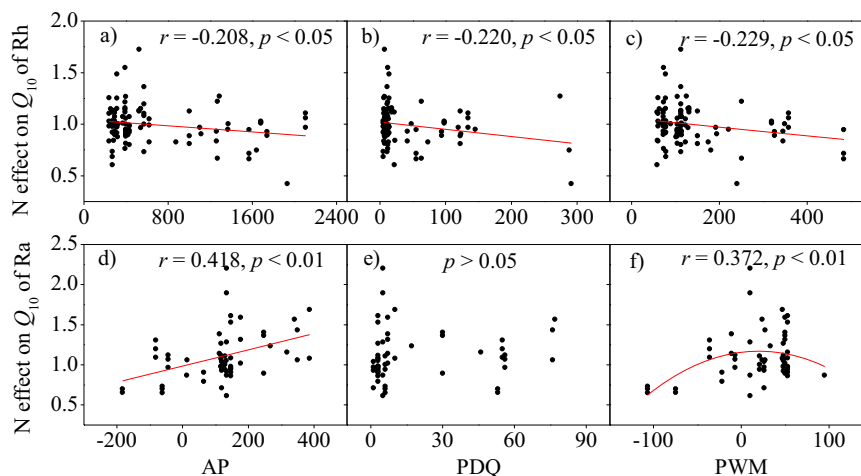


Fig. 5 Dependence of the influence of nitrogen enrichment on the temperature sensitivity of soil respiration on past rainfall conditions. The relationships between indices of precipitation from paleoclimate and nitrogen effects on the temperature sensitivity of soil heterotrophic respiration (a–c), and autotrophic respiration (d–f) across all ecosystems. AP, PWM, and PDQ denote annual precipitation, precipitation of wettest month and precipitation of driest quarter, respectively. Results of linear mixed effect model are seen in Supp. Table 9.

Ra at the global scale based on previous studies that investigated the responses of soil respiration to N addition or fertilization^{8,35,36}. Given that the average size of the N effect on the Q₁₀ values of Ra was significantly larger than 1.0 (Fig. 2), the positive linear relationship of N-enrichment effects on the Q₁₀ of Ra with latitude (Fig. 1) indicated that N enrichment had greater enhancement on the Q₁₀ of Ra in high-latitude ecosystems than in low-latitude ecosystems. In high-latitude ecosystems, the intense competition between plants and microorganisms for N was alleviated by N enrichment³⁷, stimulating the growth and turnover of plant roots and the activity of root-associated microorganisms^{6,38}. This notion has been confirmed by observations that N enrichment increases the inputs and quality of fine roots by modifying the photosynthetic rate and the belowground allocation of photosynthesis output^{36,39,40}. In addition, acidic and alkaline soils showed little difference in the mean response of the Q₁₀ of Ra to N enrichment, although the response of the Q₁₀ of Ra under N enrichment was significant in acidic soil (Fig. 2), which was derived mainly from the smaller dispersion of its dataset. However, scarce data on the pH of the studied soils weakened the conviction of this finding and limited our further exploration of the potential mechanism. This calls for an emphasis on the effect of soil pH in further investigations.

Despite the nonsignificant averaged N effects on the Q₁₀ of Rh, a low N application rate increased the Q₁₀ of Rh relative to the control treatment ($p < 0.05$; Fig. 2b), which was greatly driven by the increase in substrate availability under slight N enrichment (Supp. Fig. 4). Nitrogen fertilization increased soil carbon availability by improving photosynthesis and plant growth, ultimately benefiting the positive response of Rh to warming^{10,41}. Alternatively, excessive N input into terrestrial ecosystems may result in a decrease in soil pH (Supp. Fig. 4), which may have eliminated the enhancement effect of N enrichment by inhibiting microbial activities⁴². Therefore, clarifying the variations in the responses of the Q₁₀ of Ra and Rh to N enrichment could help to accurately estimate the ecosystem C cycle under global warming and increasing atmospheric N deposition.

Not entirely consistent with the results of meta-analysis which revealed nonsignificant overall effects of N enrichment on the Q₁₀ of Rt or Rh, the variation partitioning analysis suggested N addition exerting the greatest impacts on the Q₁₀. This is because the variation partitioning analysis takes contemporary climate and paleoclimate into account conjointly with N addition regime,

whereas meta-analysis focused on the overall effect of N enrichment on the Q₁₀ within the categorized group without considering the interactions with other predictors such as climatic factors. Although N addition explained a large proportion of the variation in the N-enrichment effects on the Q₁₀ of both Ra and Rh probably through its regulation on soil properties, the importance of climate, especially the paleoclimate, was not masked or moderated by short-term N management, exerting a strong control on the spatial variations in the responses of Q₁₀ to N enrichment (Fig. 3d–f). The greater importance of the paleoclimate than the contemporary climate in regulating the responses of Q₁₀ to N enrichment was mainly due to the legacy effect of past climate conditions on soil properties^{43,44}. For example, in a forest under a current wet climate which was previously a grassland ecosystem under a drier paleoclimate, estimations based on current climate might cause large biases in soil C dynamics. Therefore, paleoclimate was found to be a better correlate than contemporary climate with the responses of Q₁₀ to N enrichment due to its indirect impact on soil properties^{43,44}.

Our piecewiseSEM result revealed that relative to the direct effects on microbial activity and functioning, climate preferentially affects the responses of Q₁₀ to N enrichment indirectly by altering the SOC and TN contents. Variations in SOC and TN contents, which have developed slowly under the influence of paleoclimates across millennial time scales^{25,26,43,44}, greatly controlled the stabilization of the organic carbon in soil^{3,7,8,45,46}. Moreover, climate, particularly the paleoclimate, was shown to regulate ecosystem functioning by strongly influencing key ecosystem characters, such as plant and soil microbial community richness and diversity through dispersal-limited recolonization and environmental filtering^{18,19,25,47,48}, which also greatly influence the soil C dynamics in response to climate change in terrestrial ecosystems^{49,50}. A strong correlation between variables from paleoclimate and modern climate was found (Supp. Table 10), however, correlation does not imply causation. Compared with the contemporary climate, the paleoclimate explained larger amounts of variations in the response of Q₁₀ to N enrichment via the direct and/or indirect regulations on soil C dynamics and soil properties. This exactly confirms the necessity of introducing paleoclimate. In comparison with previous studies that illustrated how paleoclimates affect soil C stocks¹⁹, our study first identified the linkage between the paleoclimate and the response of Q₁₀ to N enrichment, highlighting the importance of

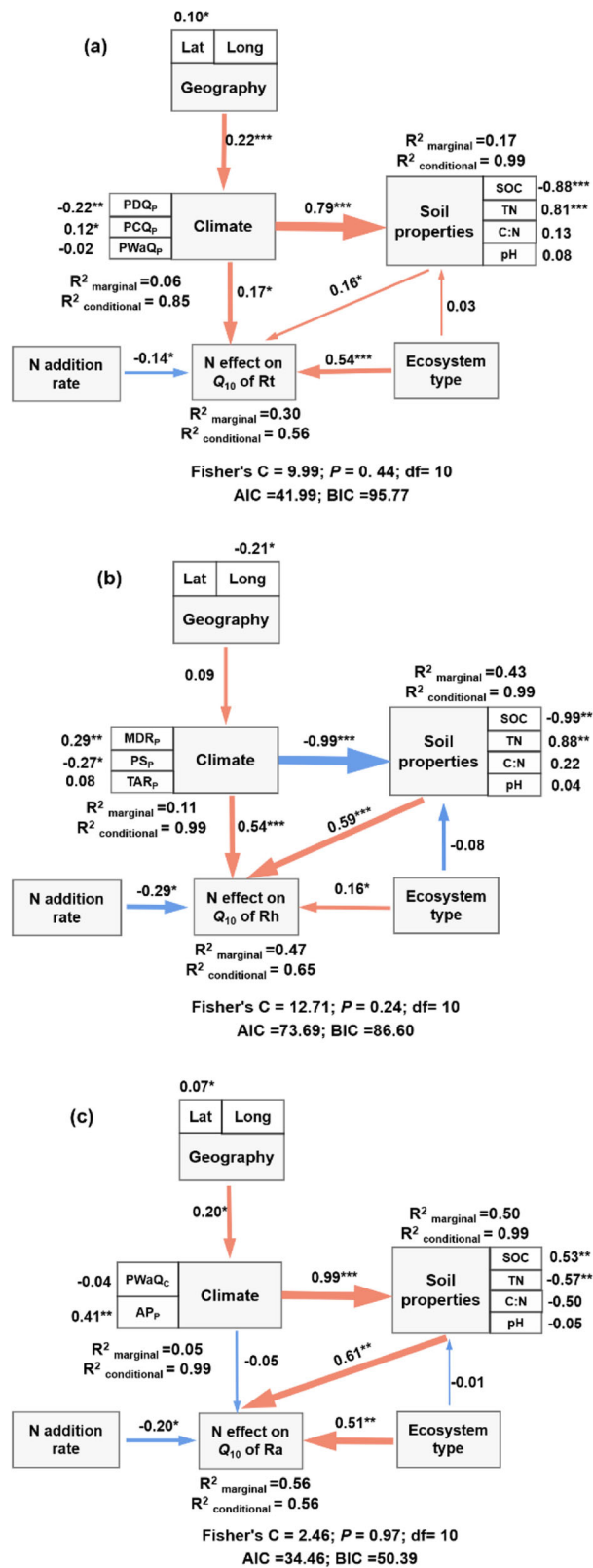


Fig. 6 Pathways of environmental and anthropogenic factors impacting the influence of nitrogen enrichment on the temperature sensitivity of soil respiration. PiecewiseSEM accounting for the direct and indirect effects of geography, climate predictors, soil properties, ecosystem types and nitrogen addition on the responses of the temperature sensitivity of total soil respiration (a), heterotrophic respiration (b), and autotrophic respiration (c) to nitrogen enrichment at the global scale. The geographical, climate and soil variables were divided into composite variable. Numbers adjacent to measured variables are their coefficients with composite variables. Numbers adjacent to arrows are path coefficients are the directly standardized effect size of the relationship. The thickness of the arrow represents the strength of the relationship. Total standardized effects of composite variables on ecosystem stability are shown in marginal and conditional R² represent the proportion of variance explained by all predictors without and with accounting for random effects of “sampling site”. Relationships between residual variables of measured predictors were not showed. Significance levels of each predictor are *p < 0.05, **p < 0.01, ***p < 0.001. Subscript c and p indicate contemporary climate and paleoclimate, separately. Detail information of bioclimatic variables were showed in Supp. Table 1.

paleoclimatic variables with high temporal resolution are required to provide more accurate and powerful prediction of soil C dynamics under global climate change.

Specifically, N-enrichment effects on the Q₁₀ of Ra and Rh are controlled by different factors from paleoclimate even when the random effects of sampling sites are considered (Fig. 6). Precipitation is a key driver of plant species filtering and biome distribution shaping; thus, it is suggested that the precipitation from paleoclimate regulated Ra by shaping plant community richness^{18,27}, and the physiology and architecture of roots, such as the turnover rate and root-related traits⁵¹, during long-term vegetation evolution. In addition, driven by the historical pattern of precipitation, dissolution, and leaching effects determined the current level of available N in the soil, which also accounted for the variations in Ra. The consequence of this impact is still detectable today, influencing the responses of the Q₁₀ of Ra to N enrichment. Temperature, serving as an important abiotic factor, exerts strong influences on the formation of SOC¹⁹. The quality and quantity of SOC, as shaped by temperature from paleoclimate, control the stabilization of SOC (i.e., Rh) and consequently regulate how N enrichment mediates the Q₁₀ of Rh¹¹. These results provide evidence for the strong interactive effects of N enrichment and paleoclimate on the Q₁₀ of different Rt components at the global scale. Overall, the novel results suggested that the paleoclimate has exerted a long-term signature on soil C dynamics, with important implications for projecting future C-climate feedback.

Although the direction and magnitude of the response of Q₁₀ to N enrichment are controversial in different ecosystem types (Fig. 2), the associated mechanisms tend to be clear, with short-term N alterations in soil pH, SOC, and the C:N ratio often demonstrated to be the most important drivers of Q₁₀^{7,10,41,52}. The variations in soil properties among ecosystems could also influence the effects of N enrichment on Q₁₀, but not significantly⁸. This impact pathway was relatively strong and became substantial only in the case of N enrichment on the Q₁₀ of Rh rather than Ra, suggesting the higher vulnerability of microbial processes than plant physiology. Therefore, the linkage of ecosystem types with the variations in the N effects on Q₁₀ (Figs. 2a, c, and 6) might be driven by the unique environments or artificial operations in ecosystems, such as high moisture and low oxygen availability in wetlands or intensive anthropogenic practices in croplands. The consideration of ecosystem type was

the paleoclimate in regulating soil C dynamics. However, we should be careful with the application of our findings regarding the regulation of paleoclimate on soil C dynamics, because the paleoclimate parameters are model-derived and not validated from proxy data⁴⁴. Further work that blends paleoclimatic model simulations with multiproxy data, as well as some other

essential for the investigation of the N effect on Q_{10} at a broad scale.

In summary, our experimental results clarified the global patterns of the Q_{10} values of total soil, heterotrophic and autotrophic respiration as well as their responses to N enrichment, and provided tentative evidence for the controlling factors of N-enrichment effects on the Q_{10} of soil respiration and its components. Furthermore, the paleoclimate explained larger variations in the N-enrichment effects on Q_{10} than the contemporary climate, indicating that the responses of Q_{10} to N enrichment were strongly regulated by the tentative legacy impacts of the paleoclimate. Furthermore, global variations in the N-enrichment effects on the Q_{10} of Ra and Rh were best predicted by precipitation and temperature from paleoclimates, respectively, revealing different mechanisms that primarily regulated the N-enrichment effects on the Q_{10} of heterotrophic and autotrophic respiration. Overall, our findings emphasize the differences in N-enrichment effects on the Q_{10} of heterotrophic and autotrophic respiration and the importance of the paleoclimate in shaping these effects. We propose that the differences in N effects on the Q_{10} of soil respiration components should be considered when modelling soil C cycling and dynamics under future scenarios of global warming and increasing N deposition.

Methods

Data sources. Peer-reviewed journal articles were searched using Web of Science (<http://apps.webofknowledge.com>) and China National Knowledge Infrastructure Database (<http://www.cnki.net>). The keywords used for the articles were: (a) soil respiration, heterotrophic respiration, autotrophic respiration, SOC decomposition or mineralization, CO₂ emission or flux, and (b) soil temperature, warming, and (c) N addition, fertilizer, fertilization, application, enrichment, or deposition published in 1990–2019.

Articles selected for this synthesis all met the following criteria. First, the experiment was conducted in the field, and Rt (Ra and Rh if available) were repeatedly measured or calculated for at least one season or three months, and the soil temperature was measured simultaneously. Second, the application rate and form of N were clearly given. Third, at least one of the soil variables (i.e., SOC, total N, total phosphorus, the C:N ratio, mineral N, available phosphorus, pH, and bulk density) was given. Fourth, Q_{10} was calculated using the following equations: $Q_{10} = e^{10\beta}$ and $Rt = \alpha \cdot e^{\beta T}$. We would use these equations to calculate the Q_{10} values if the studies only gave the data of Rt or CO₂ emission with corresponding soil temperature. Measurements from different years at the same study site by the same group were averagely calculated as one data point. When multiple measurements of Rt were conducted in the same study, we used all data to calculate the Q_{10} value. Articles with the following characteristics were excluded from this synthesis: (a) manure or compost additions; (b) soil temperature was not simultaneously measured with Rt; (c) studies conducted in the laboratory or greenhouse; (d) studies conducted in desert ecosystems. Furthermore, articles in which Q_{10} can't be well estimated ($r < 0.80$) by fitting the Rt or CO₂ flux with soil temperature were also excluded from this synthesis. Based on the above criteria, in total 168 reviewed articles (see Supplementary References) and 686 observations were selected from 1069 published papers. When the data in articles were presented in the figure, we used Getdata Graph Digitizer (version 2.26) to extract the data.

Data were extracted from selected papers, including latitude, longitude, elevation, mean annual temperature (MAT) and mean annual precipitation (MAP), Rt or CO₂ flux, SOC, total N and phosphorus, the C:N ratio, mineral N, available phosphorus, pH, and bulk density. To test the differences in the responses of Q_{10} to N enrichment, four ecosystem types (forest, cropland, grassland, and wetland), three forms of N fertilizers (NH₄NO₃, urea, and others (i.e., Ca(NO₃)₂NH₄NO₃, (NH₄)₂SO₄, KNO₃, NaNO₃, NH₄Cl)), two climate zones (subtropical and temperate), soil acidity (acidic and alkaline) were differentiated in this analysis. The tropical region was classified into subtropical zone because only few observations were obtained in tropical zones. For the same reason, boreal and alpine systems were classified into temperate ones. Measurement methods of Rt or CO₂ were divided into the static chamber and automated soil CO₂ flux system, such as Li-cor 8100. In addition, N application rates were divided into three levels: low (<5 g N m⁻² yr⁻¹), medium (5–15 g N m⁻² yr⁻¹) and high (>15 g N m⁻² yr⁻¹). Most experiments gave the geographical locations (latitude and longitude), which were shown in Supp. Fig. 1.

Paleoclimate. For all the sites with latitude and longitude surveyed in the study, nineteen standardized climatic variables (Supp. Table 1) for the contemporary climate and Last Glacial Maximum (about 22,000 years ago) climate were obtained from the Worldclim database (www.worldclim.org) and estimated from the Community Climate System Model (CCSM4; www.cesm.ucar.edu/models/

ccsm4.0/) (see ref. 19,53), respectively. For our analyses, we selected 7 out of 19 climatic variables that were not strongly correlated with the rest ($r < 0.80$; ref. 53) based on Pearson correlation analysis to avoid the multicollinearity: mean diurnal range (MDR), mean temperature of coldest quarter (MTCQ), minimum temperature of the coldest month (MinTCM), temperature annual range (TAR), annual precipitation (AP), precipitation of wettest month (PWM) and precipitation of driest quarter (PDQ).

Data analysis. In order to compare the response of the Q_{10} of Rt, Rh, and Ra to N enrichment and test whether these responses changed linearly with latitude, the effect size of N enrichment on Q_{10} were calculated as the response ratio, $RR = X_t / X_c$, where X_t and X_c are the Q_{10} values in enriched-N treatments and the control treatments⁵⁴. A 95% confidence interval (CI) of the effect size was calculated: 95% CI = $\gamma \pm 1.96$ SE, where γ and SE are the mean value and standard error of RR in each categorized group, respectively. The significant differences in the Q_{10} values of different Rt components and their responses to N enrichment among different classification groups were tested by the least significant difference multiple-comparison post hoc test after the one-way analysis of variance. Linear or quadratic regression analyses were performed to test the possible dependency of N effects on the Q_{10} of Rt and its different components on paleoclimate indices. In order to further explore the impacts of temperature and precipitation from paleoclimate on the response of Q_{10} to N enrichment, an additional linear mixed-effects model was performed with the sample site as a random factor using “nlme” package. Variation partitioning analysis based on “packfor” and “vegan” packages was performed to assess the relative importance of three groups: N addition regime (application rate, N chemical forms, and ecosystem types), contemporary climate and paleoclimate in driving global-scale variation in Q_{10} and its response to N enrichment. The “forward.sel” function was used to avoid redundancy and multicollinearity in variation partitioning analysis. To test whether the responses of the Q_{10} of Rt, Rh, and Ra to N enrichment were affected by other predictors, we also compared the differences of the responses of the Q_{10} of Rt, Rh, and Ra to N enrichment among various ecosystem types, forms and rates of N fertilizers, climate zones, detection methods, soil acidity.

To further explore the underlying mechanisms of the spatial variations in the response of Q_{10} to N enrichment, piecewise structural equation modelling (piecewiseSEM) was employed to evaluate the direct and indirect links between key ecosystem factors and N-enrichment effects on the Q_{10} of Rt and its components in our global survey. The use of SEM is particularly useful in large-scale correlative studies due to its ability to partition the causal influences among multiple variables, and separate the direct and indirect effects of model predictors⁵⁵. We constructed a priori model following ref. 18, in which spatial information (longitude, latitude), climate (contemporary climate and paleoclimate), ecosystem types (forests, cropland, wetland, and grasslands), and soil properties (e.g., SOC, total N, the C: N ratio and pH) were simultaneously accounted. We acknowledge that we might miss some effects from excluded variables on N-enrichment effects on the Q_{10} . However, we also reduce the complexity of our models, providing a more comprehensive understanding on the main direct and indirect effects of climate, soil properties, and microbial community on the response of Q_{10} to N enrichment, therefore allowing us to properly address our research question. All observed variables were divided into composite variables first and then included in SEM. In order to confirm the robustness of the relationships between key ecosystem factors and N-enrichment effects on Q_{10} , we used piecewiseSEM to account for random effects of sampling sites, providing “marginal” and “conditional” contribution of environmental predictors. These analyses were conducted using “piecewiseSEM”⁵⁶, “nlme” and “lme4” packages⁵⁷. We used the Fisher's C test to judge the goodness of the modelling results. The models were modified stepwise according to the pathway significance ($p < 0.05$) and the goodness of the model ($0 \leq \text{Fisher's } C/\text{df} \leq 2$ and $0.05 < P \leq 1.00$).

Data availability

The supporting data for the statistics and figures can be found at: <https://doi.org/10.6084/m9.figshare.16644724>.

Code availability

The R code used in this study can be found at: <https://figshare.com/s/721e1cdf608c033a1215>.

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References

- Bond-Lamberty, B. & Thomson, A. Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579–582 (2010).
- Raich, J. W., Potter, C. S. & Bhagawati, D. Interannual variability in global soil respiration, 1980–94. *Glob. Change Biol.* **8**, 800–812 (2002).

3. Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition feedbacks to climate change. *Nature* **440**, 165–173 (2006).
4. Feng, X., Simpson, A. J., Wilson, K. P., Williams, D. D. & Simpson, M. J. Increased cuticular carbon sequestration and lignin oxidation in response to soil warming. *Nat. Geosci.* **1**, 836–839 (2008).
5. Heimann, H. & Reichstein, R. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* **451**, 289–292 (2008).
6. Fang, C. et al. Impacts of warming and nitrogen addition on soil autotrophic and heterotrophic respiration in a semi-arid environment. *Agr. Forest Meteorol.* **248**, 449–457 (2018).
7. Wang, Q., Liu, S., Wang, Y., Tian, P. & Sun, T. Influences of N deposition on soil microbial respiration and its temperature sensitivity depend on N type in a temperate forest. *Agr. Forest Meteorol.* **260–261**, 240–246 (2018).
8. Zhong, Y. Q. W., Yan, W. M., Zong, Y. Z. & Shanguan, Z. P. The effects of nitrogen enrichment on soil CO₂ fluxes depending on temperature and soil properties. *Global Ecol. Biogeogr.* **25**, 475–488 (2016).
9. Yu, G. R. et al. Stabilization of atmospheric nitrogen deposition in China over the past decade. *Nat. Geosci.* **12**, 424–429 (2019).
10. Coucheney, E., Strömberg, M., Lerch, T. Z. & Herrmann, A. M. Long-term fertilization of a boreal Norway spruce forest increases the temperature sensitivity of soil organic carbon mineralization. *Ecol. Evol.* **3**, 5177–5188 (2013).
11. Jiang, J. S., Guo, S. L., Wang, R., Liu, Q. F. & Sun, Q. Q. Effects of nitrogen fertilization on soil respiration and temperature sensitivity in spring maize field in semi-arid regions on loess plateau. *Environ. Sci.* **36**, 1802–1809 (2015).
12. Wang, Q., Zhao, X., Tian, P., Liu, S. & Sun, Z. Bioclimate and arbuscular mycorrhizal fungi regulate continental biogeographic variations in effect of nitrogen deposition on the temperature sensitivity of soil organic carbon decomposition. *Land Degrad. Dev.* **32**, 936–945 (2021).
13. Schindlbacher, A., Zechmeister-Boltenstern, S. & Jandl, R. Carbon losses due to soil warming: do autotrophic and heterotrophic soil respiration respond equally? *Glob. Change Biol.* **15**, 901–903 (2009).
14. Carey, J. C. et al. Temperature response of soil respiration largely unaltered with experimental warming. *Proc. Natl Acad. Sci.* **113**, 13797–13802 (2016).
15. Lyu, M., Giardina, C. P. & Litton, C. M. Interannual variation in rainfall modulates temperature sensitivity of carbon allocation and flux in a tropical montane wet forest. *Glob. Change Biol.* **27**, 3824–3836 (2021).
16. Wang, Q. et al. Global synthesis of temperature sensitivity of soil organic carbon decomposition: latitudinal patterns and mechanisms. *Funct. Ecol.* **33**, 514–523 (2019).
17. Li, J. et al. Biogeographic variation in temperature sensitivity of decomposition in forest soils. *Glob. Change Biol.* **26**, 1873–1885 (2020).
18. Delgado-Baquerizo, M. et al. Palaeoclimate explains a unique proportion of the global variation in soil bacterial communities. *Nat. Ecol. Evol.* **1**, 1339–1347 (2017).
19. Delgado-Baquerizo, M. et al. Climate legacies drive global soil carbon stocks in terrestrial ecosystems. *Sci. Adv.* **3**, e1602008 (2017).
20. Delgado-Baquerizo, M. et al. Ecological drivers of soil microbial diversity and soil biological networks in the southern hemisphere. *Ecology* **99**, 583–596 (2018).
21. Ding, J. Y. & Eldridge, D. J. Contrasting global effects of woody plant removal on ecosystem structure, function and composition. *Perspect. Plant Ecol.* **39**, 125460 (2019).
22. Eldridge, D. J. & Delgado-Baquerizo, M. The influence of climatic legacies on the distribution of dryland biocrust communities. *Glob. Change Biol.* **25**, 327–336 (2019).
23. Pärtel, M., Chiarucci, A., Chytrý, M. & Pillar, V. D. Mapping plant community ecology. *J. Veg. Sci.* **26**, 1–3 (2017).
24. Richter, D. D. & Yaalon, D. H. “The changing model of soil” revisited. *Soil Sci. Soc. Am. J.* **76**, 766–778 (2012).
25. Lyons, S. K. et al. Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* **529**, 80–83 (2016).
26. Schmidt, M. W. I. et al. Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56 (2011).
27. Delgado-Baquerizo, M. et al. Carbon content and climate variability drive global soil bacterial diversity patterns. *Ecol. Monogr.* **86**, 373–390 (2016).
28. Maestre, F. T., Delgado-Baquerizo, M., Jeffries, T. C., Eldridge, D. J. & Singh, B. K. Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proc. Natl Acad. Sci.* **112**, 15684–15689 (2015).
29. Monger, C. et al. Legacy effects in linked ecological–soil–geomorphic systems of drylands. *Front. Ecol. Environ.* **13**, 13–19 (2016).
30. Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187 (2000).
31. Fierer, N., Colman, B. P., Schimel, J. P. & Jackson, R. B. Predicting the temperature dependence of microbial respiration in soil: a continental-scale analysis. *Glob. Biogeochem. Cy.* **20**, GB3026 (2006).
32. Peng, S., Piao, S., Wang, T., Sun, J. & Shen, Z. Temperature sensitivity of soil respiration in different ecosystems in China. *Soil Biol. Biochem.* **41**, 1008–1014 (2009).
33. Xu, Z. et al. Temperature sensitivity of soil respiration in China’s forest ecosystems: patterns and controls. *Appl. Soil Ecol.* **93**, 105–110 (2015).
34. Niu, B. et al. Warming homogenizes apparent temperature sensitivity of ecosystem respiration. *Sci. Adv.* **7**, eabc7358 (2021).
35. Janssens, I. A. et al. Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.* **3**, 315–322 (2010).
36. Yan, G. Y. et al. Sequestration of atmospheric CO₂ in boreal forest carbon pools in northeastern China: Effects of nitrogen deposition. *Agr. Forest Meteorol.* **248**, 70–81 (2018).
37. Du, E. Z. et al. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat. Geosci.* **13**, 221–226 (2020).
38. Chen, Z. M. et al. Nitrogen fertilization stimulated soil heterotrophic but not autotrophic respiration in cropland soils: A greater role of organic over inorganic fertilizer. *Soil Biol. Biochem.* **116**, 253–264 (2018).
39. Chen, F. et al. Effects of N addition and precipitation reduction on soil respiration and its components in a temperate forest. *Agr. Forest Meteorol.* **271**, 336–345 (2019).
40. Zhang, C. et al. Effects of simulated nitrogen deposition on soil respiration components and their temperature sensitivities in a semiarid grassland. *Soil Biol. Biochem.* **75**, 113–123 (2014).
41. Moinet, G. Y. K. et al. The temperature sensitivity of soil organic matter decomposition is constrained by microbial access to substrates. *Soil Biol. Biochem.* **116**, 333–339 (2018).
42. Li, Y. et al. Soil acid cations induced reduction in soil respiration under nitrogen enrichment and soil acidification. *Sci. Total Environ.* **615**, 1535–1546 (2018).
43. Sanderman, J. Comment on “Climate legacies drive global soil carbon stocks in terrestrial ecosystems”. *Sci. Adv.* **4**, e1701482 (2018).
44. Ding, J. et al. The paleoclimatic footprint in the soil carbon stock of the Tibetan permafrost region. *Nat. Commun.* **10**, 4195 (2019).
45. Gershenson, A., Bader, N. E. & Cheng, W. X. Effects of substrate availability on the temperature sensitivity of soil organic matter decomposition. *Glob. Change Biol.* **15**, 176–183 (2009).
46. Doetterl, S. et al. Soil carbon storage controlled by interactions between geochemistry and climate. *Nat. Geosci.* **8**, 780–783 (2015).
47. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377 (2012).
48. Li, J., Ziegler, S. E., Lane, C. S. & Billings, S. A. Legacies of native climate regime govern responses of boreal soil microbes to litter stoichiometry and temperature. *Soil Biol. Biochem.* **66**, 204–213 (2013).
49. Xu, M. et al. High microbial diversity stabilizes the responses of soil organic carbon decomposition to warming in the subsoil on the Tibetan Plateau. *Glob. Change Biol.* **27**, 2061–2075 (2021).
50. Du, Y. et al. The response of soil respiration to precipitation change is asymmetric and differs between grasslands and forests. *Glob. Change Biol.* **26**, 6015–6024 (2020).
51. Meier, I. C. & Leuschner, C. Leaf size and leaf area index in *Fagus sylvatica* forests: competing effects of precipitation, temperature, and nitrogen availability. *Ecosystems* **11**, 655–669 (2008).
52. Li, J., Pei, J., Pendall, E., Fang, C. & Nie, M. Spatial heterogeneity of temperature sensitivity of soil respiration: A global analysis of field observations. *Soil Biol. Biochem.* **141**, 107675 (2020).
53. Katz, M. H. *Multivariable Analysis: A Practical Guide for Clinicians and Public Health Researchers* (Cambridge Univ. Press, Cambridge, 2006).
54. Leff, J. W. et al. Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proc. Natl Acad. Sci.* **112**, 10967–10972 (2015).
55. Grace, J. B. *Structural Equation Modeling Natural Systems* (Cambridge Univ. Press, Cambridge, 2006).
56. Lefcheck, J. S. PiecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
57. Bates, D. et al. lme4: Linear mixed-effects models using Eigen and S4. *R package version 1*, 1–13 (2017).

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Author contributions

This specific study was designed by Q.K.W., with help from P.T. and S.E.L. Data extraction and statistical analyses were performed by P.T., S.E.L. and Q.K.W. P.T., and Q.K.W. wrote the first draft of the manuscript; X.C.Z., Z.L.S., X.Y., S.L.N., and T.W.C. contributed substantially to revisions.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Qingkui Wang.

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