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

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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.

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Oil respiration is the second-largest carbon (C) flux from terrestrial ecosystems to the atmosphere, ranging from 68 to 98 Pg C yr$^{-1}$, and thus plays a vital role in regulating atmospheric CO$_2$ concentrations. The response of total soil respiration (Rt) to elevated temperature, which is referred to as temperature sensitivity ($Q_{10}$), regulates the magnitude and direction of global C migration and its feedback to climate change$. A growing body of evidence suggests that terrestrial C dynamics are severely affected by atmospheric nitrogen (N) deposition$, which has introduced a great amount of reactive N into the terrestrial system and is predicted to persist in the long term$. In addition, evidence to support such broad-scale feedback is only correlative rather than causative, so multiple lines of evidence are needed. Yet, how Qt$_{10}$ 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 Qt$_{10}$ to N enrichment has been widely investigated at individual sites (e.g., ref. 6,10), with increases and decreases in the Qt$_{10}$ 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 Qt$_{10}$ as well as the comparison of N deposition effects between forest and grassland ecosystems at a regional scale were revealed recently. These previous studies have advanced our understanding of the mechanisms underlying the N-enrichment effect on Qt$_{10}$. 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 Qt$_{10}$ 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 Qt$_{10}$ values of these components may exhibit different responses to N enrichment, as they are controlled by different mechanisms, which further increases the difficulty in assessing the role of Rt in global C cycling under global climate change. Therefore, understanding how Qt$_{10}$ 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 warming.

Mounting evidence suggests that geographical variations in Qt$_{10}$ are primarily driven by climate predictors, particularly the mean annual temperature (MAT) and mean annual precipitation (MAP)$^{14-17}$. For example, the Qt$_{10}$ 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 Qt$_{10}$ was also found to positively correlate with MAT at a global scale$^{16}$. 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 Qt$_{10}$ 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 time$^{24}$. The physiochemical characteristics of the soil, such as pH, SOC, and nutrient contents, have developed slowly under the influence of past climates across millennia time scales$^{25,26}$. Therefore, the paleoclimate is expected to be potentially associated with the response of Qt$_{10}$ 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 Qt$_{10}$ of soil respiration$^{5,30,31}$, but whether the global-scale effects of N enrichment on the Qt$_{10}$ 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 Qt$_{10}$ needs to be examined to enhance our understanding of soil C cycle–climate change feedbacks under global environmental change$^{32}$. Here, we synthesized the data collected from 168 published papers based on field N enrichment experiments. The global patterns of the Qt$_{10}$ 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 Qt$_{10}$ with climatic and edaphic factors. In this study, we addressed the following questions: (1) How does N enrichment affect the Qt$_{10}$ of Rt and its components at the global scale? (2) Whether the paleoclimate could predict the N-enrichment effects on Qt$_{10}$ better than the contemporary climate? (3) How does the paleoclimate directly and indirectly regulate the effects of N enrichment on the Qt$_{10}$ of Rt and its components?

### Results

**Global patterns of Qt$_{10}$ values and their response to N enrichment.** Across all observations, the Qt$_{10}$ values of Rt and Rh were positively related to latitude (Fig. 1a, b), but no apparent correlation was found between the Qt$_{10}$ of Ra and latitude (Fig. 1c). The responses of the Qt$_{10}$ values of Rt and Ra to N enrichment expressed positive linear correlations with latitude (Fig. 1a, c), while the response of the Qt$_{10}$ values of Rh to N enrichment was not related to latitude (Fig. 1b). Nitrogen enrichment enhanced the Qt$_{10}$ of Ra on average by 10.6% ($p < 0.05$; Fig. 2c), which was applied to both inorganic (NH$_4$NO$_3$) and organic (urea) N applications. In contrast, only NH$_4$NO$_3$ significantly increased the Qt$_{10}$ of Rt ($p < 0.05$; Fig. 2a). A low rate of N application increased the Qt$_{10}$ of Rh by 9.0% relative to the control treatment ($p < 0.05$; Fig. 2b). The Qt$_{10}$ 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 Qt$_{10}$ were almost the same in acidic and alkaline soils, although the response of the Qt$_{10}$ 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 Qt$_{10}$ to N enrichment, with slightly positive effects of N enrichment on the Qt$_{10}$ of Ra in temperate zones (Supp. Fig. 3).

**Mechanisms underlying the variation in Qt$_{10}$ in response to N enrichment.** The variation partitioning results showed that N enrichment could explain the largest unique fraction of the variations in Qt$_{10}$ and the N-enrichment effects on Qt$_{10}$ at the global scale, with an exception of the variations in the N-enrichment effects on Qt$_{10}$ 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 Qt$_{10}$ of Rt (4.90% versus 0.81%), Rh (2.67% versus 1.19%) and Ra (8.97% versus...
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
with previous studies that explored the spatial variations in the $Q_{10}$ of Rt 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 Rt and Rh that linearly increased with latitude (Fig. 1a, b); however, this pattern was not revealed for Ra (Fig. 1c). This finding indicates that the latitudinal distributions of the $Q_{10}$ of Ra and Rh were different and that the spatial variations in the $Q_{10}$ of Rt were mainly contributed by $Q_{10}$ of Rh. Moreover, the lack of apparent correlation between the $Q_{10}$ of Ra and latitude might be partly attributed to the indirect measurement of Ra via separating Rh from Rt, which could introduce great variation in Ra. Strikingly, the sensitivities of Rt and Rh 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 Rt in colder regions was higher than that in warmer regions14,33. 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 Rt and its heterotrophic component to elevated temperature may potentially decline under global warming1,34.

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.
Ra at the global scale based on previous studies that investigated the responses of soil respiration to N addition or fertilization. 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 enrichment, stimulating the growth and turnover of plant roots and the activity of root-associated microorganisms. 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. 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. 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 activities. 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. 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.

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, greatly controlled the stabilization of the organic carbon in soil. 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, which also greatly influence the soil C dynamics in response to climate change in terrestrial ecosystems. 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 stocks, our study first identified the linkage between the paleoclimate and the response of Q10 to N enrichment, highlighting the importance of...
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 data\textsuperscript{44}. Further work that blends paleoclimatic model simulations with multiproxy data, as well as some other 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 $Q_{10}$ 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\textsuperscript{18,27}, and the physiology and architecture of roots, such as the turnover rate and root-related traits\textsuperscript{51}, 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 $Q_{10}$ of Ra to N enrichment. Temperature, serving as an important abiotic factor, exerts strong influences on the formation of SOC\textsuperscript{19}. 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 $Q_{10}$ of Rh\textsuperscript{11}. These results provide evidence for the strong interactive effects of N enrichment and paleoclimate on the $Q_{10}$ 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 $Q_{10}$ 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 $Q_{10}$\textsuperscript{7,10,41,52}. The variations in soil properties among ecosystems could also influence the effects of N enrichment on $Q_{10}$ but not significantly\textsuperscript{8}. This impact pathway was relatively strong and became substantial only in the case of N enrichment on the $Q_{10}$ 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 $Q_{10}$ (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
essential for the investigation of the N effect on Q10 at a broad scale. In summary, our experimental results clarified the global patterns of the Q10 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 Q10 of soil respiration and its components. Furthermore, the paleoclimate explained larger variations in the N-enrichment effects on Q10 than the contemporary climate, indicating that the responses of Q10 to N enrichment were strongly regulated by the tentative legacy impacts of the paleoclimate. Furthermore, global variations in the N-enrichment effects on the Q10 of Ra and Rh were best predicted by precipitation and temperature from paleoecologies, respectively, revealing different mechanisms that primarily regulated the N-enrichment effects on the Q10 of heterotrophic and autotrophic respiration. Overall, our findings emphasize the differences in N-enrichment effects on the Q10 of heterotrophic and autotrophic respiration and the importance of the paleoclimate in shaping these processes. We propose that the differences in N effects on the Q10 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. Forth, Q10 was calculated using the following equations: 

\[ Q_{10} = e^{10β} \] and 

\[ RT = α + βT \]

We would use these equations to calculate the Q10 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 Q10 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 Q10 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 Q10 to N enrichment, all of the studies only gave the data of Rt or CO2 emission with corresponding soil temperature. The same reason, boreal and alpine systems were classified into temperate ones. The same reason, the same climatic groups were tested by the least significant difference multiple-comparison test. For all the sites with latitude and longitude surveyed in the study, Q10 was calculated as the response ratio, RR = X1/X2, where X1 and X2 are the Q10 values in enriched-N treatments and the control treatments. A 95% confidence interval (CI) of the effect size was calculated: 95% CI = y ± 1.96 SE, where y and SE are the mean value and standard error of RR in each categorized group, respectively. The significant differences in the Q10 values of different Rt components and their responses to N enrichment among the different classification groups were tested by the least significant difference multiple-comparison 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 Q10 of Rt and its different components on paleoclimate indices.

Data availability. In order to compare the response of the Q10, Rt, Rh and Ra to N enrichment and test whether these responses changed linearly with latitude, the effect size of N enrichment on Q10 was calculated as the response ratio, RR = X1/X2, where X1 and X2 are the Q10 values in enriched-N treatments and the control treatments. A 95% confidence interval (CI) of the effect size was calculated: 95% CI = y ± 1.96 SE, where y and SE are the mean value and standard error of RR in each categorized group, respectively. The significant differences in the Q10 values of different Rt components and their responses to N enrichment among different classification groups were tested by the least significant difference multiple-comparison 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 Q10 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 Q10 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 Q10 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 Q10 of Rt, Rh, and Ra to N enrichment were affected by other predictors, we also compared the differences of the responses of the Q10 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 Q10 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 Q10 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 it makes it possible to explore both the direct and indirect effects of model predictors. 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 Q10. 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 Q10 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 Q10, 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 ≤ Fisher’s C/D ≤ 2 s 0 ≤ p ≤ 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/721e1cd608e033a1215.

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Author contributions
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Competing interests
The authors declare no competing interests.

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