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A global synthesis of patterns in soil organic matter and temperature sensitivity along the altitudinal gradient

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Although it is important to determine how the global carbon (C) cycle is responding to climate change in our three-dimensional Earth, variation in the soil organic matter (SOM) and temperature sensitivity (Q_{10}) of soil respiration along the altitudinal gradient remains unclear globally. This study explored spatial variability in SOM and Q_{10} and its regulatory mechanisms from a three-dimensional perspective. We collected SOM and Q_{10} datasets from published studies for 0−10 cm soil depth along elevational gradients of mountain ranges globally. We found that the SOM content in most mountains changed significantly with increasing altitude; unexpectedly, these changes with altitude significantly differed across different climate zones. Specifically, the SOM content increased with increasing altitude in tropical and subtropical regions, while it decreased with increasing altitude in temperate and plateau regions. Climate factors (mean annual temperature and mean annual precipitation) and soil properties (total N content, C/N ratio, and pH) together accounted for 83% of spatial variation in SOM with altitude. Q_{10} values, under both laboratory incubation and *in situ* studies, did not significantly correlate with altitude, and no apparent global patterns were detected (mean: 2.07); however, Q_{10} was regulated by variation in soil substrate quality along altitudinal gradients, to some extent. In the context of global climate change, this new information on SOM and Q_{10} in relation to the altitude at a global scale might enhance our understanding of soil C−climate feedbacks.

KEYWORDS

soil organic matter, organic carbon, soil respiration, altitude gradient, temperature sensitivity
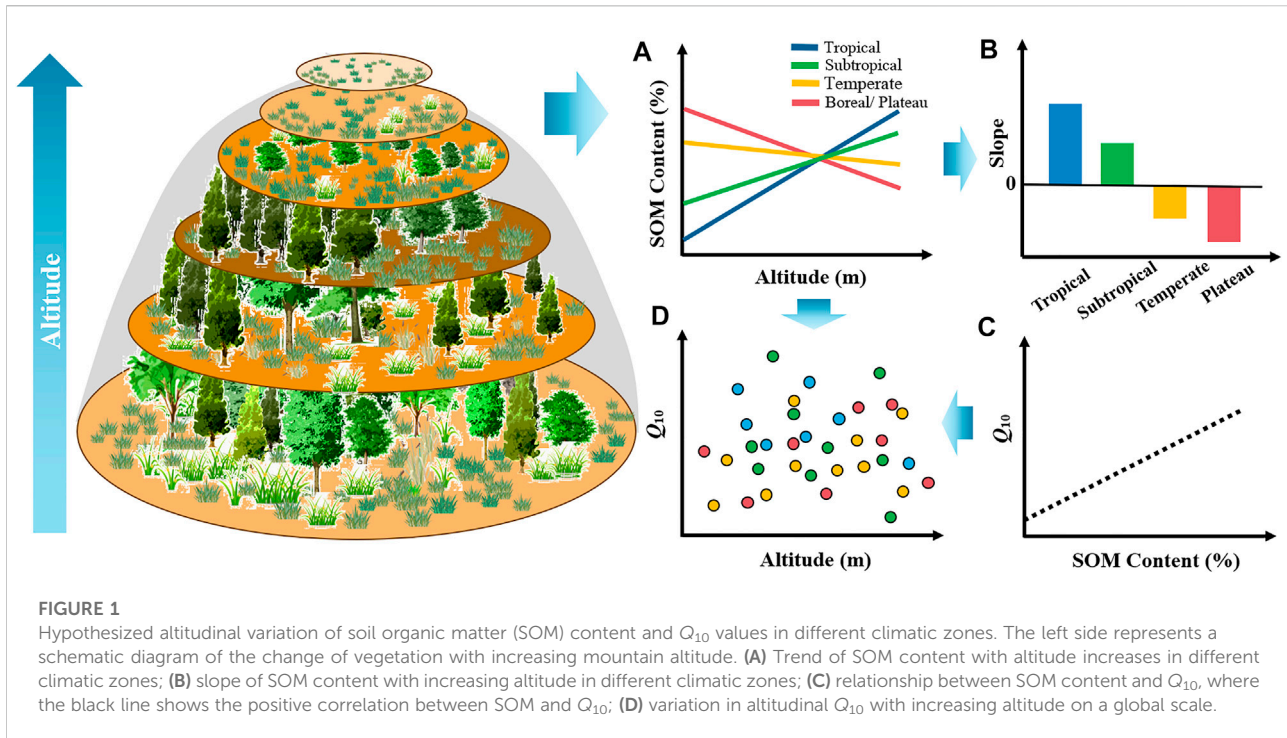
1 Introduction

Soil organic matter (SOM) is an important pool of carbon (C) in terrestrial ecosystems, being approximately 2 to 3-fold that of atmospheric and biotic C, respectively (Jackson et al., 2017). SOM supports many vital ecosystem services, from the provision of food and fiber, to regulating climate and water cycles, regenerating fertility, and supporting the immense biodiversity of soils (Lehmann and Kleber, 2015). CO_2 emitted from SOM decomposition is the second-largest CO_2 flux in the land–atmosphere interface and is influenced by various factors, including climate (Hawkes et al., 2017), temperature (Li et al., 2017a), moisture (Yan et al., 2018), substrate quality (Liu et al., 2021), substrate effectiveness (Li et al., 2022), and microbes (Karhu et al., 2014). Among these factors, temperature is the most important, regulating SOM decomposition (Davidson and Janssens, 2006), and thus, it is essential to understand SOM dynamics, especially with the background of global warming (Davidson and Janssens, 2006). It is reported that approximately 25% of the land surface of the Earth is covered by mountainous regions (Korner, 2007), are particularly vulnerable to climate warming as they combine a steep climatic gradient, and thus, are widely used to investigate soil C–climate feedbacks (Korner, 2007). Although many studies have investigated trends in C, nitrogen, and their stoichiometry along altitudinal gradients in individual mountain ranges, our understanding of changes in SOM along elevational gradients at the global scale is greatly limited. SOM stocks as a result of C input from primary productivity and output through microbial decomposition. Temperature and precipitation are major influences on vegetation productivity and important factors affecting SOM decomposition (Wang et al., 2016; Li et al., 2017a), which may also lead to inconsistent trends in SOM along the altitudinal gradient in different climatic zones around the globe, as changes in latitude and longitude also imply variability in temperature and precipitation (Tashi et al., 2016; Yin et al., 2021). Therefore, it is particularly important to investigate the global pattern in altitudinal SOM content and the factors influencing its decomposition, and this contributes to our understanding of the global C cycle.

The temperature sensitivity of SOM decomposition is often quantified using Q_{10}, which is defined as the proportional increase in the CO_2 emission rate for a 10°C increase in temperature, and the Q_{10} is considered to be a key parameter in depicting the magnitude and direction of soil C–climate feedbacks. Minor variation in Q_{10} can result in large differences in estimates of soil C dynamics (Todd-Brown et al., 2013). However, in most ecological models, researchers often consider Q_{10} as a fixed value to simplify them, rising uncertainty in C–climate model predictions (Jian et al., 2018). Therefore, it is important and urgent, to quantitatively analyze the spatial patterns (horizontal and elevational) of Q_{10} and its drivers to optimize terrestrial C cycle models (Jian et al., 2018).

Spatial horizontal variation in Q_{10} has been widely demonstrated at regional and global scales (Liu et al., 2017; Li et al., 2020b; Li et al., 2020c). These studies have greatly advanced our current understanding of the response of SOM decomposition to temperature variations and underlying mechanisms at different scales. However, approximately 25% of the land surface of Earth is covered by mountains; thus, the three-dimensional zonality of terrestrial ecosystems is a common feature, globally (Sundqvist et al., 2013). Changes in altitude affect temperature and precipitation, similar to latitudinal variation in terrestrial ecosystems to some extent (Korner, 2007). However, the trend in the variation in Q_{10} with altitude at a global scale remains unclear, despite altitude potentially being an important source of spatial variability in Q_{10}. Furthermore, studies on how Q_{10} varies with altitude have been sparse to date, and those that have been conducted have generally focused on a single mountain range in a given climate zone (Niklińska and Klimek, 2007; Zimmermann and Bird, 2012; Gutierrez-Giron et al., 2015; Wang et al., 2016; Li et al., 2017b). To our knowledge, there is no integration of relevant studies across multiple climate zones, which also hinders our understanding of Q_{10} variation at spatial scales. Therefore, exploring how Q_{10} responds to altitude changes can help us to more comprehensively understand the influencing factors and variability patterns of Q_{10}, and thus provide a basis for building a more reasonable C-climate model, which is especially important in the context of global warming.

Accordingly, in this study, we collected data from 323 studies on the distribution of SOM along altitudinal gradients, and 18 laboratory studies and 36 *in situ* studies on Q_{10}. The primary objectives of this study were to 1) explore variation in SOM content and Q_{10} along the altitudinal gradient at zonal and global scales and 2) elucidate the mechanism underlying this effect. The latitudinal pattern of SOM globally showed that terrestrial SOM levels increase progressively with latitude (Stockmann et al., 2015), due to the effects of vegetation and other environmental factors (Sundqvist et al., 2013). Similar to latitudinal patterns, changes in altitude are related to changes in climate factors, which, in turn, alter SOM (Sundqvist et al., 2013). Tropical and subtropical regions have favorable hydrothermal conditions and high vegetative productivity, which is highly favorable for soil microbial activity. Because microbes decompose SOM rapidly, SOM content is lower at lower altitudes in tropical and subtropical areas. However, temperature decreases with increasing altitude, limiting microbial activity; consequently, the rate of SOM decomposition decreases, and SOM from plants is more strongly sequestered in the soil in tropical and subtropical areas (Sundqvist et al., 2013). Therefore, SOM content increases with altitude. Nevertheless, in temperate and plateau regions, lower MAT and MAP limit soil microbial activity and inhibit the microbial decomposition of SOM, such that basal SOM values are relatively high in these regions. However, as the altitude increases, relatively poor hydrothermal conditions result in lower plant biomass and net primary production (Li et al., 2021a), especially in alpine regions

FIGURE 1
Hypothesized altitudinal variation of soil organic matter (SOM) content and Q_{10} values in different climatic zones. The left side represents a schematic diagram of the change of vegetation with increasing mountain altitude. **(A)** Trend of SOM content with altitude increases in different climatic zones; **(B)** slope of SOM content with increasing altitude in different climatic zones; **(C)** relationship between SOM content and Q_{10}, where the black line shows the positive correlation between SOM and Q_{10}; **(D)** variation in altitudinal Q_{10} with increasing altitude on a global scale.

(Sundqvist et al., 2013). Consequently, C return to soil is lowered, particularly when coupled with the slow rate of microbial decomposition of litter in nutrient-deficient, low-temperature, dry environments (Vitousek et al., 1994); thus, SOM gradually decreases with increasing altitude (Vitousek et al., 1994). Therefore, we hypothesized that it is difficult to establish a uniform association between SOM content and altitude on a global scale (Figures 1A,B); however, it is possible, to distinguish SOM in different climate zones to establish a potential association.

Q_{10} is often considered as an intrinsic property of a given pool independent of the environmental conditions and this is how it is classically represented in models (Davidson and Janssens, 2006). Although Q_{10} is also influenced by environmental factors such as temperature and moisture, these environmental factors mainly affect Q_{10} by shaping microbial activity, traits (Li et al., 2021b), and substrate availability (Wang et al., 2016). Additionally, numerous studies have verified from different perspectives that substrate quality and availability control the responses of SOM decomposition to warming (Davidson and Janssens, 2006; Conant et al., 2008a; Conant et al., 2008b; Davidson et al., 2012; Wang et al., 2018; Liu et al., 2021), and the Arrhenius kinetics and Michelis–Menten kinetics were used to describe the effect of substrate quality and availability on Q_{10}. Therefore, we suggest that Q_{10} along the altitudinal gradient is also controlled by the soil substrate quality (e.g., SOC, C/N, and pH). As mentioned earlier, we inferred that there is no uniform relationship between SOM and altitude on a global scale.

Based on the relationship between soil substrate quality/ quantity and Q_{10} (Figure 1C), we, therefore, hypothesized that the relationship between Q_{10} and altitude may be different in different climatic zones and there is no uniform relationship on a global scale (Figure 1D).

2 Material and methods

2.1 Literature survey and data extraction

We collected peer-reviewed articles on SOM and Q_{10} from the Web of Science (www.webofknowledge.com) and China National Knowledge Infrastructure (http://epub.cnki.net) from 1984 to 2020. In total, 323 articles describing the distribution of SOM along altitudinal gradients were obtained; especially, there were 20, 117, 145, and 41 articles for tropical, subtropical, temperate, and plateau regions, respectively (Supplementary Table S2). SOM content was selected for 10-cm depth soil. The original data were first extracted from reported tables or graphs using GetData Graph Digitizer (http://getdata-graph-digitizer.com). Simultaneously, other auxiliary data, such as geographic information (i.e., longitude, latitude, and altitude), climate data (i.e., mean annual temperature [MAT] and mean annual precipitation [MAP]), and soil chemical properties (i.e., SOM, SOC [SOM and SOC can be interconverted with a factor of 1.724], soil total N [TN], and C: N ratio [C/N]) were obtained from the published literature. Unfortunately, studies

conducted in boreal regions were not found. The Qing–Tibet Plateau is called the "third pole of the world," and has certain similarities with the boreal zone in terms of climate, especially regarding temperature. Therefore, the plateau was taken as being representative of the boreal zone in this study.

To avoid the influence of complex ecological factors in the field, we collected laboratory studies that used optimal conditions (without temperature and moisture limitations) in incubation experiments; that is, at an incubation temperature of 10–30°C and 50–70% field water holding capacity (Liu et al., 2017). The Q_{10} value was selected for 10-cm soil depth because this surface layer has the highest respiration activity of all soil layers (Liu et al., 2017). Most Q_{10} values were directly obtained from published studies. Only some Q_{10} values were indirectly obtained from respiration data using Eq. 1:

$$SR = \alpha \times e^{\beta T}, \tag{1}$$

where SR is the measured soil respiration rate, T is the measured soil temperature, and coefficients α and β are fitted parameters. The Q_{10} value was determined using Eq. 2:

$$Q_{10} = e^{10\beta}. \tag{2}$$

A total of 18 studies on the distribution of Q_{10} along altitudinal gradients were collected, of which, 1, 8, and 9 studies were conducted in tropical, subtropical, and temperate regions, respectively (Supplementary Table S3). Each study included at least three altitudinal levels. We also selected *in situ* studies on Q_{10} along altitude gradients. In total, 169 datasets were derived from 36 published studies, of which 3, 5, 18, and 10 studies were from tropical, subtropical, temperate, and plateau regions, respectively (Supplementary Table S4).

2.2 Data assembly

In total, 2,370 SOM datasets were obtained from 323 published studies with 20, 117, 145, and 41 studies for tropical, subtropical, temperate and plateau regions, corresponding to 185, 778, 1,079, and 328 datasets, respectively. Of these, only 1,909 datasets from 246 published studies contained SOM, geographical information, climate information, and soil chemical properties, with 11, 101, 112, and 22 studies for tropical, subtropical, temperate, and plateau regions, corresponding to 96, 706, 859, and 248 datasets, respectively. A total of 83 datasets from 18 published studies were selected for the Q_{10} analysis, of which 3, 28, and 52 datasets were from tropical, subtropical, and temperate regions, respectively. These studies contained information on climate and soil properties. Furthermore, 169 datasets of Q_{10} data were obtained from 36 published studies, including 12, 19, 92, and 46 datasets from tropical, subtropical, temperate, and plateau regions, respectively. The geographical distribution of the sites where SOM and Q_{10} were collected is shown in Figure 2.

2.3 Statistical analyses

We analyzed the relationship between SOM and altitude using 2,370 SOM datasets. However, as mentioned earlier, because only some of the SOM datasets contained both SOM data, geographic information, climatic information, and soil properties, we used only the 1,909 datasets containing such information in our analysis of the factors influencing SOM. The Kolmogorov–Smirnov test was used to evaluate data normality. When the data did not conform to a normal distribution, a logarithmic transformation or normalization process was followed, so that they better resembled a normal distribution. Differences in Q_{10} across climatic regions were analyzed using one way analysis of variance (ANOVA), with the least significant difference (LSD) for multiple comparisons. Regression analysis was performed to evaluate the association between SOM and Q_{10} with altitude, soil properties, and climate factors. We used a structural equation model (SEM) to quantify the relative importance of direct and indirect factors predicting SOM and Q_{10} values, respectively. Before implementing the SEM, we first normalized and standardized each variable (i.e., SOM, Q_{10}, TN, C/N ratio, and pH) using min-max normalization transformation (actual value–min)/(max–min), which was performed on the entire dataset and for all climatic zones (Li et al., 2020c). To conduct the SEM, we first established *a priori* model based on our existing knowledge of the direct and indirect effects of climate (i.e., MAT and MAP) and soil properties (i.e., SOM, TN, C/N, and pH) on SOM and Q_{10} values. Through the stepwise exclusion of nonsignificant paths in the initial model, we selected a final model that best fitted our data. The adequacy of the model was assessed using the chi-square (χ^2) test, goodness-of-fit (GFI) index, and root mean squared error of approximation (RMSEA) index (Liu et al., 2017; Li et al., 2020c). Favorable model fits were ascertained from no significant difference in the χ^2 test ($p > 0.05$), high GFI (>0.9), and low RMSEA (<0.05).

Statistical analyses and correlations were performed using SPSS Statistics 13 (IBM, Chicago, IL, United States). SEM analysis was conducted using AMOS 21.0 software (IBM, Chicago, IL, United States). Graphs were plotted using Origin software (Version 8.5; Northampton, MA, United States) and ESRI ArcGIS software (Version 10.2; Redlands, CA, United States). A statistical probability of $p < 0.05$ determined significance.

3 Results

3.1 Variation in SOM with increasing altitude in different climatic regions globally

Within the SOM datasets we collected, 61.8% of these studies observed a significant relationship between SOM content and
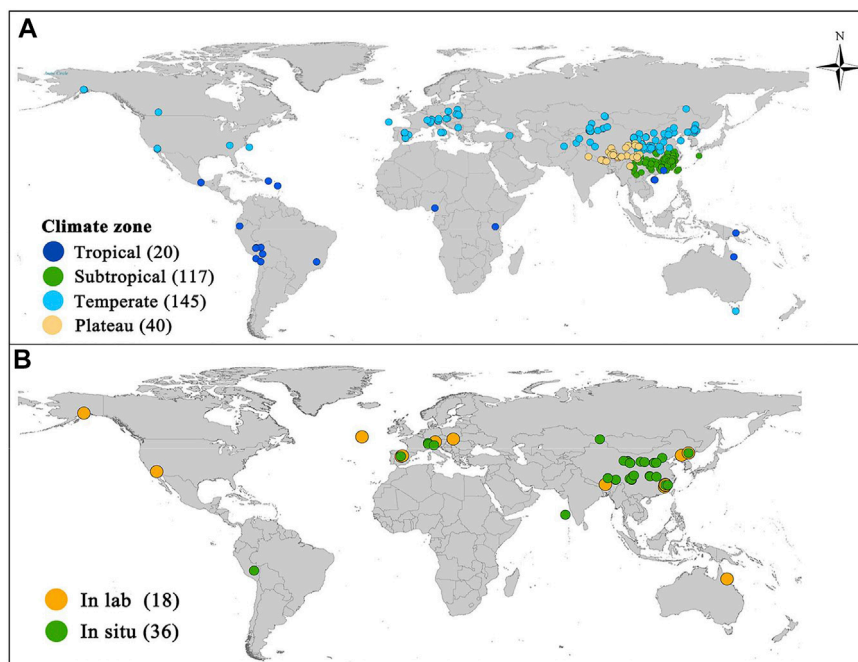
FIGURE 2
Geographical distributions of the study sites. The numbers in parentheses indicate observations of soil organic matter **(A)** and Q_{10} **(B)** values of soil respiration for each climatic zone. Some sites are very close to each other, resulting in corresponding symbols overlapping to some extent.

altitude (Supplementary Table S1); however, we observed no significant associations between altitude and SOM content on a global scale ($p > 0.05$; Figure 3E). Changes in SOM with altitude were significant among different climate zones. Specifically, SOM content increased with altitude in tropical ($R^2 = 0.38$, $p < 0.001$; Figure 3A) and subtropical regions ($R^2 = 0.15$, $p < 0.001$; Figure 3B), but decreased with altitude in temperate ($R^2 = 0.03$, $p < 0.001$; Figure 3C) and plateau regions ($R^2 = 0.08$, $p < 0.001$; Figure 3D). Moreover, on comparing the slope of SOM content with changes in altitude for different climate zones, the slope displayed a decreasing (positive to negative) trend from tropical to plateau regions (Figure 3F).

3.2 Variation in Q_{10} with increasing altitude in different climatic regions globally

For the laboratory studies, Q_{10} values changed from 1.37 to 3.15 (mean 2.07) with an altitudinal gradient. The mean values were 2.02, 1.97, and 2.13 for tropical, subtropical, and temperate zones, respectively, and were not significantly different among zones (Supplementary Figure S1). We did not observe a significant relationship between Q_{10} values and altitude for the laboratory studies, either in different climatic zones or overall ($p > 0.05$; Figure 4). For *in situ* studies, Q_{10} values changed from

0.90 to 5.74 (mean 2.76) with an altitudinal gradient (Supplementary Figure S2A). We also did not observe a significant relationship between Q_{10} values and altitude in *in situ* studies on a global scale ($p > 0.05$; Supplementary Figure S2B), but the Q_{10} in different climate zones was significantly correlated with altitude except for tropical regions ($p < 0.05$; Supplementary Figures S2C–F) and was similar to the trend obtained for SOM content with altitude in corresponding climatic zones.

3.3 Drivers of SOM and Q_{10} variation along the altitudinal gradient

SOM content was significantly influenced by TN, with a clear linear increase in SOM with increasing TN ($R^2 = 0.65$, $p < 0.001$; Supplementary Figure S3A). Moreover, SOM content significantly increased with increasing C/N ($R^2 = 0.08$, $p < 0.001$; Supplementary Figure S3B) and MAP ($R^2 = 0.03$, $p < 0.001$; Supplementary Figure S3E), but significantly decreased with falling pH ($R^2 = 0.07$, $p < 0.001$; Supplementary Figure S3C); however, the associations between SOM and MAT were not significant ($p > 0.05$; Supplementary Figure S3D). SEM analysis revealed a strong association between climate and soil properties. Among all variables, MAT, TN, C/N, and pH had a direct,
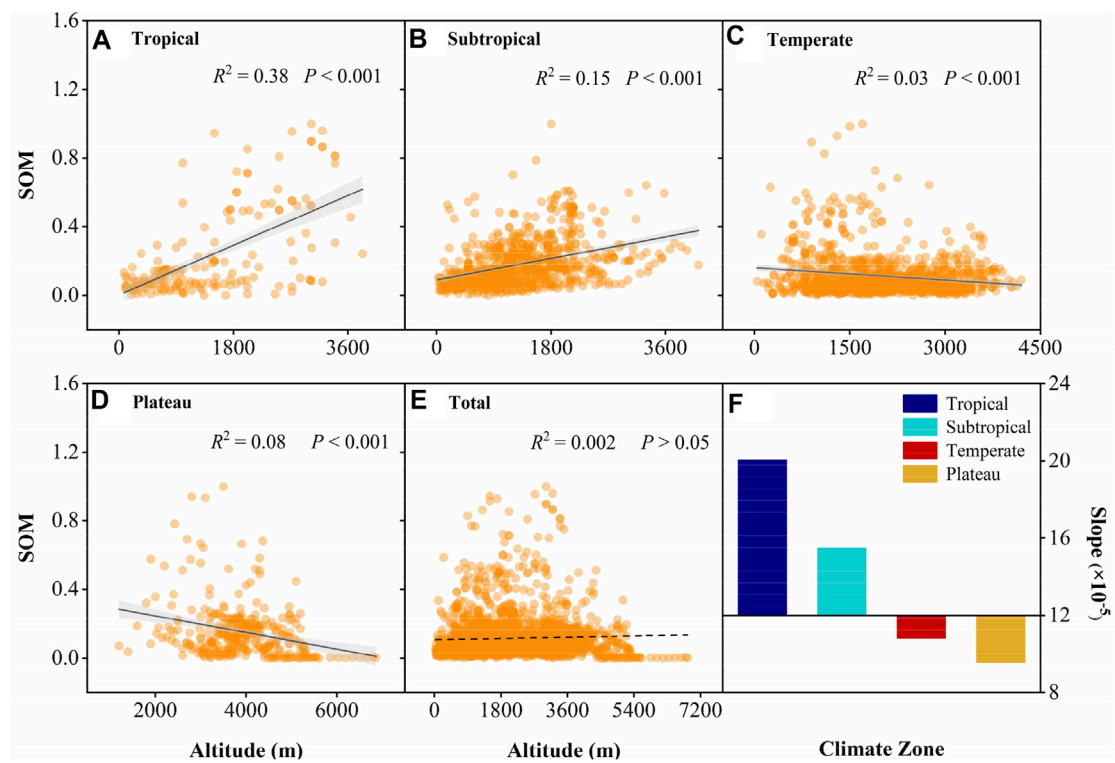
FIGURE 3
Relationship between soil organic matter content and altitude across climatic zones. **(A–E)** Trends in SOM content with altitude in different climatic zones, respectively. **(F)** Slopes of SOM content in comparison to altitude in different climatic zones. Tropical: $n = 185$, subtropical: $n = 778$, temperate: $n = 1,079$, plateau: $n = 328$, total: 2,370; SOM data in the figure were normalized by min-max normalization. Shaded areas indicate the 95% confidence interval.

significant association with the SOM content, while MAP indirectly influenced spatial variation in SOM. These five variables together accounted for 83% of SOM variation (Figure 6A). Furthermore, TN had the most marked effect, followed by C/N and pH, as indicated by standardized total effects in predicting global SOM values (Figure 6B).

Q_{10} was significantly and negatively associated with the MAT ($R^2 = 0.08$, $p < 0.05$; Figure 5E); however, the association between Q_{10} and MAP was not significant ($p > 0.05$; Figure 5F). Moreover, Q_{10} values significantly increased with increasing SOM content ($R^2 = 0.13$, $p < 0.001$; Figure 5A), TN ($R^2 = 0.06$, $p < 0.05$; Figure 5B), and C/N ($R^2 = 0.08$, $p < 0.01$; Figure 5C). However, Q_{10} values were significantly affected by soil pH and linearly decreased with increasing pH ($R^2 = 0.05$, $p < 0.05$; Figure 5D). SEM analysis revealed that soil properties (SOM, C/N ratio, and pH) could predict Q_{10} values, all of which had a significant direct effect on Q_{10} variability (Figure 6C). Climatic factors (including MAT and MAP) did not significantly and directly influence Q_{10}; rather, they influenced Q_{10} indirectly by influencing soil properties. All variables accounted for 27% of Q_{10} variation; SOM was the primary influencing factor, accounting for 31% of the total variation, followed by pH and MAT (Figure 6D).

4 Discussion

4.1 Trends in SOM with altitude depend on climatic zones

Soil C sequestration is the uptake of atmospheric CO_2 by terrestrial ecosystems through plant photosynthesis and its conversion and long-term storage in the soil. However, differences in soil type, above-ground vegetation, and climate result in significant differences in soil C storage capacity across regions (Stockmann et al., 2015). Spatial patterns in SOM at different latitudes globally revealed that terrestrial SOM levels increase progressively with latitude and are affected by vegetation, temperature, and precipitation (Minasny et al., 2017). Similarly, changes in altitude are associated with changing climate factors, which, in turn, alter SOM. This study showed that changes in SOM with altitude were not consistent across different climatic zones and this is supported by a previous study (Yin et al., 2021). For instance, SOM content increased with increasing altitude in tropical and subtropical regions but decreased with increasing altitude in temperate and plateau regions. This finding contrasts with the conventional
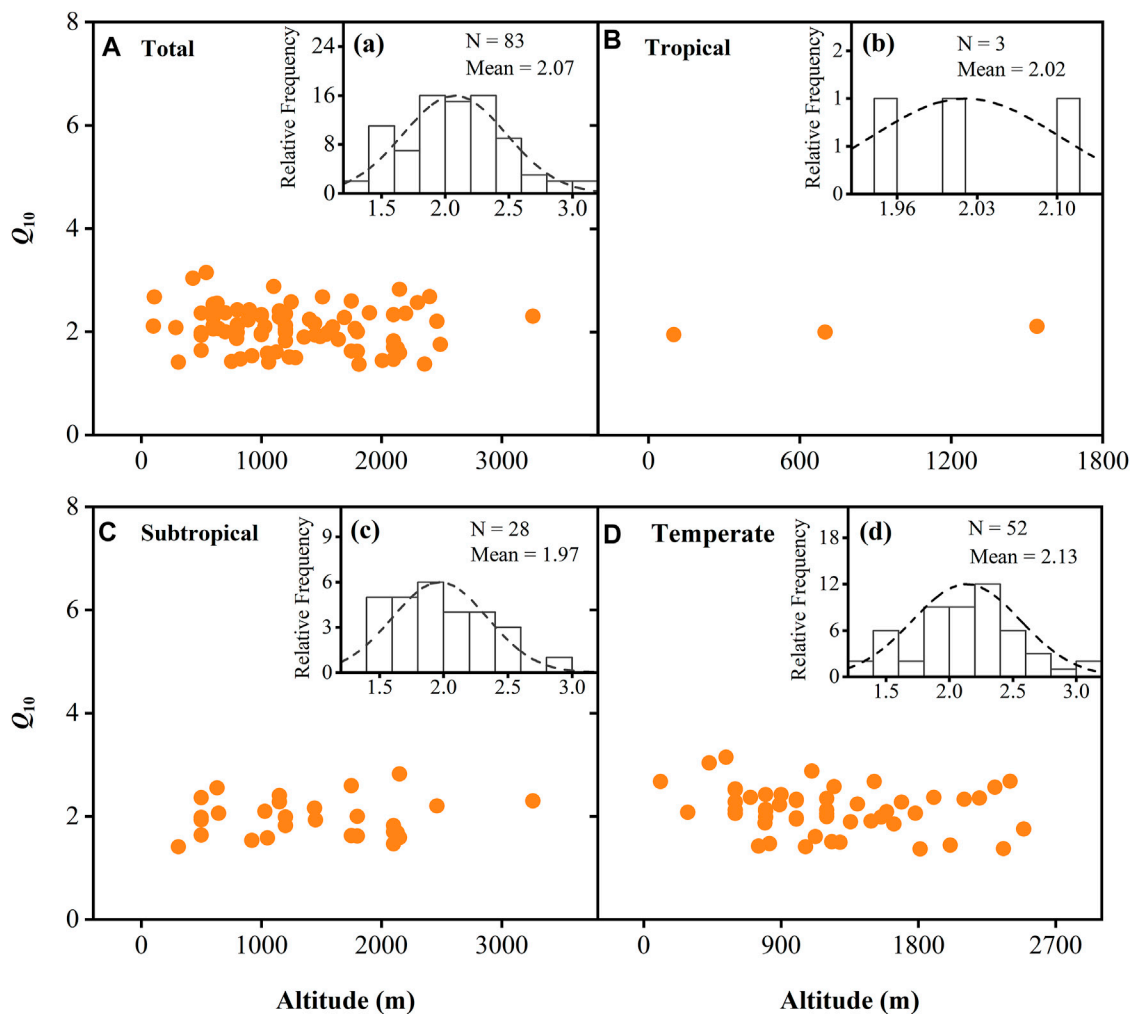
FIGURE 4
Variation in temperature sensitivity (Q_{10}) of soil organic matter decomposition with altitude in different climatic zones. **(A)** Trends in Q_{10} values with altitude on a global scale; **(B–D)** Trends in Q_{10} content with altitude in tropical **(B)**, subtropical **(C)**, and temperate regions **(D)**, respectively. **(A–D)** Frequency distribution of Q_{10} in the corresponding regions, respectively.

view that SOM content increases with altitude, mainly because changes in altitude also affect plant productivity and carbon inputs to the soil (Davidson et al., 2000), leading to different trends in SOM content with altitude in different climatic zones.

Suitable hydrothermal conditions at low elevations in the tropics and subtropics facilitate high net primary productivity in plants and favors microbial activity; consequently, microbial decomposition of SOM is faster and does not favor C sequestration, resulting in lower SOM content (Schimel et al., 1994; Sundqvist et al., 2013). However, as elevation increases, lower temperatures limit microbial activity, with the rate of microbial decomposition of SOM slowing and it being possible for organic matter from plants to be more strongly sequestered in soil; thus, SOM content increases with altitude

(Dai and Huang, 2006; Sundqvist et al., 2013). Nevertheless, in temperate and plateau regions, lower MAT limits soil microbial activity and slows the decomposition of SOM, such that the basal SOM contents are relatively high in these regions (Dai and Huang, 2006). However, as altitude increases, relatively poor hydrothermal conditions result in lower plant biomass and productivity (Vitousek et al., 1994), especially in alpine regions. This phenomenon coupled with the slow rate of microbial decomposition of litter in nutrient-deficient soil at low temperature, results in lower quantities of organic matter returning to the soil. Moreover, there also is characterized by low diversity of the plant community and a harsh environment in high-altitude sites (Feng et al., 2021), the transfer strategy of microbes (e.g., r-/K-trait) may also play a key role (Dai et al.,
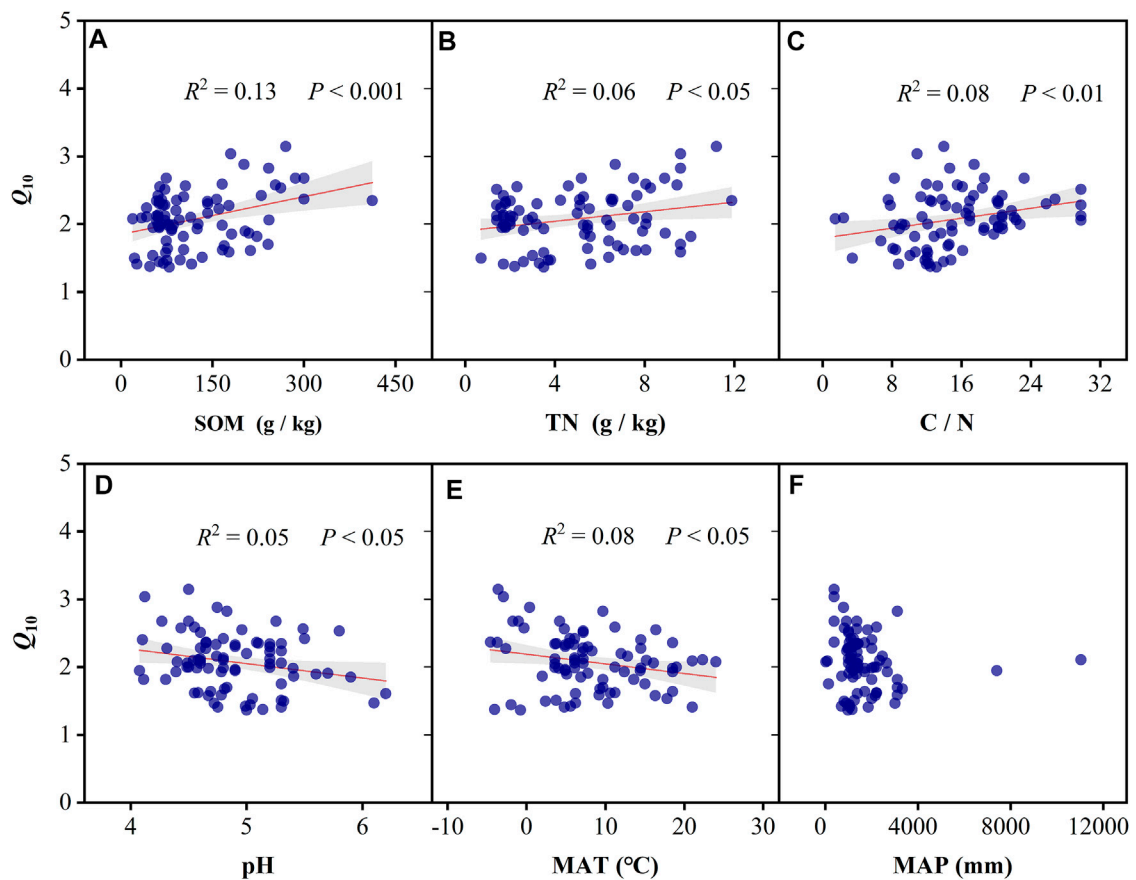
FIGURE 5
Q_{10} value of soil respiration in relation to soil properties and climatic factors on a global scale (n = 83). **(A–F)** Relationships between Q_{10} and SOM, TN, C/N, pH, MAT, and MAP, respectively. SOM, soil organic matter; TN, total nitrogen; C/N, ratio of carbon and nitrogen; MAT, mean annual temperature; MAP, mean annual precipitation. Shaded areas indicate the 95% confidence interval.

2021; Feng et al., 2021). Thus, SOM content gradually decreases with increasing altitude (Davidson et al., 2000). Therefore, it is difficult to establish a uniform association between SOM content and altitude on a global scale; however, it is possible to identify differences in SOM among different climate zones to establish associations.

Soil properties (TN, C/N, and pH) and climate factors (MAT and MAP) explained the variation in SOM in the current study (Figure 6; Supplementary Figure S3). A significant correlation between soil N content and SOM content was previously reported (Spain, 1990). First, N-containing compounds and humus account for a large part of SOM, with N elements including amino acids and polypeptides being the primary components of humus (Spain, 1990); thus, soil TN reflects the size of SOM, to a large extent. Soil C/N tends to characterize the coupling of SOM and TN and is an important indicator of the potential of soil N mineralization and whether SOM decomposition is limited by soil N (Hu et al., 2001). In

general, when the C/N ratio is lower, N is more available to microbes, making it more favorable for SOM decomposition. Conversely, the microbial function during SOM decomposition is limited by soil N (Hu et al., 2001), leading to the accumulation of SOM. Therefore, soil C/N has a significant positive effect on SOM. The soil pH affects the turnover and accumulation of SOM by influencing the soil microbial activity and community structure (Motavalli et al., 1995; Staddon et al., 1998).

Climate, especially temperature and precipitation, largely determines vegetation cover, quantity and quality of organic residues entering the soil, and the rate of SOM mineralization and litter decomposition; consequently, it also determines the turnover of SOM (Davidson et al., 2000). Many studies have reported a significant negative correlation between the MAT and SOM content (Ganuza and Almendros, 2003; Lemenih and Itanna, 2004). However, this study did not find any significant association between the MAT and SOM on a global scale. This phenomenon might be explained by the fact that lower
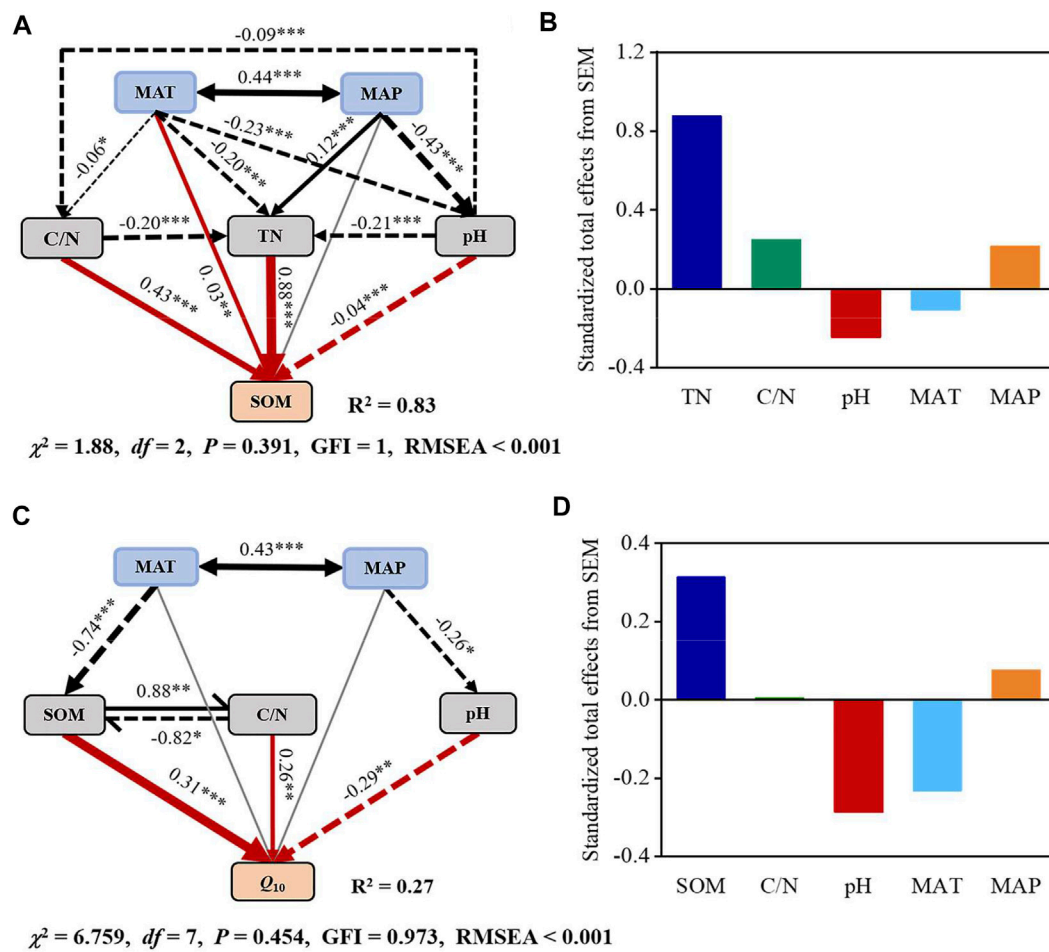
FIGURE 6
Structural equation model (SEM) on the direct and indirect effects of SOM **(A)** and Q_{10} **(C)** and standardized total effect (direct plus indirect effects) derived from SEM **(B,D)** on a global scale. Solid and dashed lines indicate positive and negative effects, respectively; the gray line indicates that the relationship is not significant at the 0.05 level; line thickness represents the magnitude of the path coefficient. The numbers adjacent to arrows are standardized path coefficients, indicating the effect size of the relationship. MAT, mean annual temperature; MAP, mean annual precipitation; SOM, soil organic carbon; TN, total nitrogen; C/N, ratio of carbon and nitrogen. Goodness-of-fit statistics are shown in the model. $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$.

temperatures imply lowered C input, despite favoring soil C storage (Yin et al., 2021). Therefore, the relationship between the MAT and SOM content over the altitudinal gradient depends on the climatic region in which it is located. Specifically, attention still needs to be paid to the effect of temperature on the balance of organic matter input and decomposition in the region where it is located. Moreover, these results indicate a positive correlation between SOM content and MAP, supporting previous studies (Dai and Huang, 2006; Homann et al., 2007). Generally, vegetation grows rapidly with higher net primary production in humid and warmer climate zones; consequently, there is a higher input litter to the soil. In addition, higher precipitation favors the decay and decomposition of falling litter, accelerating the input of external C to the soil, resulting in higher SOM content (Dai and Huang, 2006; Sundqvist et al., 2013).

4.2 No clear variation in Q_{10} along the altitudinal gradient at different scales

This study showed that Q_{10} ranged from 1.37–3.15 (mean 2.07) along the altitudinal gradient on a global scale, with no significant differences among climate zones. Some studies previously reported that Q_{10} increases gradually with altitude (Zimmermann and Bird, 2012; Wang et al., 2013); however, other studies reported that Q_{10} values show no discernible trend with altitude (Niklińska and Klimek, 2007; Xu et al., 2010; Xu et al., 2014; Wang et al., 2016). The contrasting results of these previous studies may be due to the fact that these studies focused only on separate mountain ranges in different climatic regions. Our study detected no consistent variation in Q_{10} along the altitudinal gradient on the global scale (Figure 4A). First, belowground

ecological processes in different climatic zones were influenced by different climate factors (Colman and Schimel, 2013). Q_{10} is influenced by various factors such as climate (Li et al., 2020b) and soil properties (Liu et al., 2017), which further contribute to the complexity of Q_{10}. Second, this study showed that SOM is the primary factor influencing spatial variation in Q_{10} along altitude (Figures 5, 6); however, trends in SOM content with altitude were inconsistent across climate zones (Figure 3); thus, environmental and soil properties jointly lead to the uncertainty in Q_{10} with altitude at a global scale.

Moreover, our evaluation of *in situ* studies also supported the uncertainty in Q_{10} with altitude at a global scale (Supplementary Figure S2B). Specifically, Q_{10} increased with altitude in subtropical regions and decreased with altitude in temperate and plateau regions. This finding was consistent with the trend obtained for SOM content with altitude. Although CO_2 released from SOM decomposition is only a partial source of CO_2 from soil respiration, microbial respiration displays a stronger response to changing temperature than root respiration (Lin et al., 2010). Thus, this phenomenon might also reflect uncertainty in the global-scale variation of Q_{10} along the altitudinal gradient, to some extent and further corroborates our finding that variation in Q_{10} is regulated by the substrate quality of the soil.

The SEM analysis revealed that spatial variation in Q_{10} with an altitude gradient was directly influenced by soil properties (i.e., SOM, C/N, and soil pH) and indirectly influenced by climate factors (MAT and MAP) (Figure 6C). Together, these factors accounted for 27% of spatial variation in Q_{10}. Q_{10} decreased with increasing MAT (Figure 5E), supporting previous studies (Zheng et al., 2009; Xu et al., 2015; Liu et al., 2017; Li et al., 2020a; Li et al., 2020b; Li et al., 2020c). The negative relationship between Q_{10} and MAT may be explained by the relative increase of enzyme activity diminishing as temperature increases (Schipper et al., 2014). Moreover, the macromolecular rate theory indicates that the net increase in soil respiration is relatively lower at higher temperatures (Schipper et al., 2014), causing Q_{10} to decline with increasing temperature. Additionally, temperature effects on soil substrate and microbial properties (e.g., K-/r-traits) may also have an impact on Q_{10} (Liu et al., 2017; Li et al., 2021b). The current study showed that areas with higher SOM and C/N also had higher Q_{10} values (Figure 5). This phenomenon was attributed to SOM being the primary substrate for soil respiration, with the quantity/quality of substrate strongly influencing the composition of the microbial community (Knorr et al., 2005; Tan et al., 2020). Furthermore, soils with higher SOM content have higher decomposable C content and microbial biomass (Colman and Schimel, 2013). Therefore, ecosystems with higher SOM content generally have a greater potential for CO_2 efflux and higher Q_{10} (Zheng et al., 2009; Li et al., 2022).

N is an important factor for the life-sustaining activities of soil microorganisms and it is a limiting factor for microbial SOM decomposition (Hu et al., 2001). Consequently, it strongly influences the activity of soil microbes. Thus, higher N content enhances the decomposition rate of SOM. Moreover, soil C and N content was closely coupled, accumulating synergistically (Gärdenäs et al., 2011). Accordingly, soil N content also revealed a significant positive correlation with Q_{10} (Figure 5B). Overall, these findings advance our current understanding of the regional variation in Q_{10} along altitudinal gradients and how it may be driven by global warming. Since trends in SOM and Q_{10} with altitude vary across different climate zones, future studies should incorporate this variation.

4.3 Limitations and outlook

This study is the first to demonstrate variation in SOM content and Q_{10} along the altitudinal gradients across different climate zones at a global scale and the mechanism underlying this effect; however, some limitations existed. First, few studies have been conducted on soil respiration C dynamics along altitudinal gradients, with existing studies primarily focusing on temperate regions; thus, other regions require more focused studies, especially in the tropical and boreal zones. Second, the existing literature provides insufficient data on the factors influencing Q_{10}, with many important factors (including soil texture and soil microbes) not being accounted for (Colman and Schimel, 2013). However, changes in altitude generate variations in biotic and abiotic factors over a smaller latitudinal and longitudinal range. This phenomenon made it difficult to obtain missing data from the International Soil Reference and Information Center (ISRIC) database. As a result, there was insufficient data on Q_{10} variation in the SEM analysis. Therefore, these effects require more comprehensive evaluation in future studies, by screening similar soil properties to improve the predictive capability of geographic patterns in soil C–climate feedback. Furthermore, because of the complexity of the field environment, we focused on Q_{10} experiments in a laboratory setting (i.e., heterotrophic respiration). However, autotrophic respiration of plants is an important part of soil respiration, with changes in temperature impacting this. Moreover, the contributions of autotrophic and heterotrophic respiration to total soil respiration may vary with the climate zone and ecosystem, and the underlying regulatory factors may also differ, which should be considered in future studies.

5 Conclusion

This global synthesis is the first to provide information on altitudinal patterns and regulatory mechanisms of SOM and Q_{10}, through a comprehensive assessment at the global and regional levels. Unexpectedly, altitude-dependent trends of SOM and Q_{10} differed in different climate zones. However, a positive

correlation between SOM and Q_{10} and C/N–Q_{10} indicates that SOM content is the primary predictor of Q_{10} for elevational soil respiration on a global scale. Furthermore, based on the negative relationship between the MAT and Q_{10}, this suggests a greater potential for soil C loss in colder regions and C-stock-rich soil in the north, in contrast to warmer regions, in response to global warming. Overall, variation in SOM and Q_{10} along altitudinal gradients differed across climate zones, advancing our understanding of geographical variations and regulatory mechanisms of Q_{10} at local to global spatial scales. Our findings could be applied to improve the predictive accuracy of soil C–climate feedback models on a global three-dimensional scale.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material; further inquiries can be directed to the corresponding authors.

Author contributions

NH and CX designed this study; CL collected the dataset, performed statistical analyses, prepared figures and tables, and drafted the manuscript with inputs from NH, CX, and ML; NH and LX reviewed and revised the manuscript and all authors contributed to revisions.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.959292/full#supplementary-material

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