



Relationship between basal soil respiration and the temperature sensitivity of soil respiration and their key controlling factors across terrestrial ecosystems

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Abstract

Purpose The purposes of this study are to characterize the relationship between basal soil respiration at 0 °C (R_0) and the temperature sensitivity (Q_{10}) of soil respiration and climate, soil, and vegetation factors and to establish R_0 and Q_{10} models.

Materials and methods We compiled R_0 and Q_{10} and variables (i.e., climate factors, soil properties, and vegetation characteristics) that were measured in various terrestrial ecosystems.

Results and discussion The results showed that both R_0 and Q_{10} could generally be fitted by a normal distribution curve across various ecosystems, but they varied greatly among the different ecosystems. The lowest median R_0 and Q_{10} appeared in the desert, while the highest median R_0 and Q_{10} appeared in the deciduous broad-leaf forest and deciduous needle-leaf forest ecosystems, respectively. The relationship between R_0 and Q_{10} across different soil depths varied among the different ecosystems, with the highest and lowest R^2 occurring in the cropland ($R^2=0.701$) and evergreen needle-leaf forest ($R^2=0.095$), respectively. A model that included Q_{10} , fine root production and the ratio of soil organic carbon to total nitrogen (TN) explained 75.0% ($R^2=0.750$) of the variation in R_0 , with a P value less than 0.001. Q_{10} was further expressed as a model ($R^2=0.663$, $P<0.001$) including annual precipitation, mean air temperature, TN, bulk density, and leaf area index.

Conclusions Our R_0 models can potentially be used to improve terrestrial carbon cycle models by considering the comprehensive effects of Q_{10} and soil and vegetation factors.

Keywords Basal respiration · Carbon quality · Temperature sensitivity (Q_{10}) · Climate · Soil properties · Vegetation characteristics

1 Introduction

Global warming due to greenhouse gas emissions has raised worldwide concern (Canadell et al. 2007). CO_2 is one of the most important greenhouse gases, and the increase in atmospheric CO_2 is related to the disturbance of the global

carbon (C) cycle (Friedlingstein et al. 2014). Soil respiration, second to gross primary productivity, is the largest C flux from soils to the atmosphere and an important component of the global C cycle (Raich and Schlesinger 1992). Temporal fluctuations in soil respiration may impact the magnitude of terrestrial-atmosphere C budgets and thus the CO_2 concentrations in the atmosphere (Bond-Lamberty et al. 2018). Modelling the seasonal patterns in soil respiration may help to investigate the processes of the global C cycle. Field-measured soil respiration is generally divided into heterotrophic and autotrophic components, which are mainly influenced by soil microorganisms and roots, respectively (Bhanja et al. 2019; Haghighi et al. 2021).

The main determinant of the temporal variations in soil respiration is soil temperature, which is often measured when measuring soil respiration (Nottingham et al.

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2020). Numerous studies have shown that an exponential model adequately explains the seasonal variations in soil respiration in most ecosystems (Johnston and Sibly 2018). The basal soil respiration at 0 °C (R_0) in the exponential model has been considered an indicator of soil C quality, while Q_{10} is the soil temperature sensitivity of soil respiration and can be calculated by the parameter of the exponential term (Conant et al. 2008a; Xu et al. 2012). The “C quality–temperature” theory points out the relationship between R_0 and Q_{10} (Bosatta and Ågren 1999; Fierer et al. 2005). This theory is based on the temperature- and enzyme-associated first-order kinetics equation and indicates that recalcitrant organic C has higher temperature sensitivity as well as for soil respiration at low temperature than for soil respiration at a higher temperature. A negative relationship between the quality of soil C respired and Q_{10} is expected since the enzyme-associated reactions metabolizing simple soil C substrates generally have a lower net activation energy than the reactions involved in complex and low-quality C substrates (Fierer et al. 2006; Reichstein et al. 2000). Several studies have confirmed the negative relationship between R_0 and Q_{10} in individual and regional studies (Conant et al. 2008b, 2011; Ding et al. 2016). R_0 and Q_{10} may be potentially impacted by the balance of various soil C pools of different quantities (Bahn et al. 2008; February et al. 2020). However, the relationship between R_0 and Q_{10} across various terrestrial ecosystems remains unknown, which may limit the applicability of terrestrial C models to simulate seasonal C dynamics. In addition, an increasing temperature due to global warming can cause substantial C emissions from terrestrial soils. Characterizing the relationship between R_0 and Q_{10} may improve the accuracy of temperature-associated soil respiration models under the scenario of global warming.

Although the climate and soil factors (e.g., temperature, precipitation, and soil C) that potentially control the spatial and temporal variations in Q_{10} have been examined in several previous studies (Bailey et al. 2018; Haaf et al. 2021; Xu et al. 2015), knowledge of the magnitude of R_0 and its key controlling factors is still lacking. A large number of measurements focusing on soil respiration and relevant climate, soil, and vegetation factors have been carried out globally, which enable us to compare R_0 and Q_{10} and explore their key controls across different ecosystems. R_0 may be influenced by controlling factors that are different from soil respiration, as respiration at 0 °C reveals relatively low soil biological reactivity. Water and nutrient availabilities, which are mainly influenced by precipitation and soil conditions in the field, respectively, may exert less effect on R_0 at the freezing point than at higher temperatures (Hursh et al. 2017; Wang et al. 2021). The comprehensive effects of climate, soil, and vegetation variables on the coupling relationship between R_0 and Q_{10} have not been well investigated.

We compiled the basal respiration at 0 °C and the Q_{10} value of the seasonal variations in annual soil respiration and relevant driving variables (i.e., site information and climate factors, soil properties, and vegetation characteristics) that were measured in various terrestrial ecosystems. The reason for the criterion that annual soil respiration should be measured is that the R_0 and Q_{10} models established in this study can potentially be used for modelling the seasonal variations in soil respiration over a whole year. The first objective of this study was to investigate the distribution patterns of R_0 and Q_{10} in the different ecosystems. The second objective was to analyze the relationship between R_0 and Q_{10} in the different ecosystems and to model R_0 and Q_{10} based on the potential climate, soil, and vegetation controlling factors.

2 Materials and methods

2.1 The dataset

The dataset of the R_0 and Q_{10} values of the annual variations in soil respiration was collected from the literature published in the journals of the Science Citation Index in English and China National Knowledge Infrastructure in Chinese. The dataset has been updated based on a global soil respiration dataset (Chen et al. 2010, 2020). The collected soil respiration data were obtained from the annual field measurements across ten terrestrial ecosystem types: broad-leaf and needle-leaf mixed forest (BNMF), cropland, deciduous broad-leaf forest (DBF), deciduous needle-leaf forest (DNF), desert, evergreen broad-leaf forest (EBF), evergreen needle-leaf forest (ENF), grassland, shrubland, and tundra. Wetlands were not included in the dataset because anaerobic soil conditions are required to produce CO₂ under water compared with nonwetland soils, and the water layer may impede CO₂ emissions from soils to the atmosphere (Nishimura et al. 2008). The site information and climate, soil, and vegetation factors are shown in Table S1. As shown in Table S1, most studies used infrared gas analyzer (IRGA) and gas chromatography methods for measuring soil respiration. The IRGA and gas chromatography methods are classical and have been widely used to determine soil respiration (e.g., Davidson et al. 1998; Franco-Luesma et al. 2020; Wang and Wang 2003). The alkali absorption method was used in a few measurement sites, and this method has been calibrated by authors in their studies (e.g., Raich 1998). Therefore, the instruments and methods for measuring soil respiration were generally consistent over 20 years. The soil and vegetation factors used in this study were compiled based on the soil physical and chemical properties and vegetation characteristics at the soil respiration measurement sites in the literature. These soil and vegetation factors were common in the field of soil and vegetation investigations and could be measured

using relatively easy methods. Therefore, the methods used to determine the soil and vegetation factors could be considered to be consistent.

The R_0 and Q_{10} of the annual variations in soil respiration are calculated on the basis of an exponential model [Eq. (1)] (Lloyd and Taylor 1994).

$$R_{s_s} = R_0 e^{aST_s} \quad (1)$$

R_{s_s} and ST_s in the model represent the seasonally measured soil respiration and soil temperature, respectively, and a is a parameter. R_0 is basal respiration at 0 °C (i.e., C quality) (Fierer et al. 2005). Q_{10} is calculated based on Eqs. (1) and (2):

$$Q_{10} = e^{10a} \quad (2)$$

As shown in Table S1, R_0 and Q_{10} were classified into three main categories according to the depths (i.e., 5 cm, 10 cm, and other depths) where the soil temperature was measured. Other information on the measurement sites included the geographical location, measurement period, annual soil respiration, climate, soil properties, and vegetation characteristics, and these variables are compiled in Table S1. The abbreviations of the variables are shown in Table 1. If the climate factors AP and MAT were unavailable in the literature, they were obtained from the University of Delaware precipitation and air temperature database (https://psl.noaa.gov/data/gridded/data.UDel_AirT_Precip.html).

2.2 Data analysis

The R_0 and Q_{10} at 5 cm, 10 cm, and other depths where the soil temperature was measured were fitted by a normal curve to characterize the distribution patterns of the two variables. The R_0 and Q_{10} at all depths in each ecosystem were compared using a box-and-whisker plot. The Duncan test was used to compare the significance of R_0 and Q_{10} differences between the different ecosystems. The relationships between R_0 and Q_{10} in each ecosystem were analyzed by a nonlinear or linear regression model across the different soil depths. The relationships between R_0 and potential influential factors (i.e., Q_{10} , FR, LF, soil respiration, C/N, and PD) in all ecosystems across the different soil depths were analyzed using a nonlinear or linear regression model, as these six variables among the climate, soil, and vegetation factors were mostly correlated with R_0 . The relationships between variables R_0 , Q_{10} , climate, soil, and vegetation factors in all ecosystems were explored using a heatmap of Pearson's correlations. R_0 was modelled based on the controlling factors Q_{10} , FR, and C/N using a multiple regression analysis. A model including potential controlling factors using multiple regression analysis was further used to model Q_{10} . A bootstrap method was used

to estimate the modelling errors of the multiple regression analysis. The threshold of variance inflation factors to test the multicollinearity of potential controlling factors was less than 5.0, and the tolerance was greater than 0.18. The modelling performance was evaluated by a linear regression relationship between the observed and modelled R_0 or Q_{10} values (Pineiro et al. 2008). The R^2 , P , RMSE (root mean squared error), ME (model efficiency), MAE (mean absolute error), AIC (Akaike information criterion), and BIC (Bayesian information criterion) (Burnham 2011; Janssen and Heuberger 1995; Schwarz 1978) were also used to evaluate the modelling performance of the R_0 and Q_{10} models. The RMSE, ME, MAE, AIC, and BIC are calculated using the equations in Table 2. We used structural equation modelling to estimate causal relationships among the key controlling factors and R_0 and Q_{10} across all ecosystems (Pearl 2000).

3 Results

3.1 The variations in R_0 and Q_{10}

Both R_0 and Q_{10} could be generally fit by a normal distribution curve (Fig. 1a, b). The μ and σ values for the normal distribution curve of R_0 were 0.708 and $0.431 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The μ and σ values for the normal distribution curve of Q_{10} were 2.471 and 0.995, respectively. The median R_0 was 0.536, 0.604, 0.684, 0.526, 0.296, 0.549, 0.691, 0.460, and $0.571 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the BNMF, cropland, DBF, DNF, desert, EBF, ENF, grassland and tundra, and shrubland ecosystems, respectively (Fig. 1c). The median Q_{10} was 2.390, 1.750, 2.233, 3.100, 1.323, 2.109, 2.145, 2.753, and 2.946 in the BNMF, cropland, DBF, DNF, desert, EBF, ENF, grassland and tundra, and shrubland ecosystems, respectively (Fig. 1d). The desert had the lowest median R_0 and smallest range ($0.259 \mu\text{mol m}^{-2} \text{s}^{-1}$) across the different ecosystems, while the DBF had the highest median R_0 and largest range ($3.355 \mu\text{mol m}^{-2} \text{s}^{-1}$). Similar to R_0 , the median Q_{10} was lowest in the desert. The DNF had the highest median Q_{10} and largest range (3.894). The Duncan test indicated that the mean R_0 was significantly ($P < 0.05$) higher in the DBF than in the grassland and tundra and desert. The mean R_0 in the desert was lowest among the different ecosystems. The mean Q_{10} was significantly ($P < 0.05$) higher in the DNF than in other ecosystems except for grassland and tundra and shrubland. The mean Q_{10} was significantly ($P < 0.05$) higher in the BNMF than in the EBF, cropland and desert. The mean Q_{10} was significantly ($P = 0.006$) higher in the EBF than in the desert.

Table 1 Categories of site information and climate, soil and vegetation factors compiled in the database

Abbreviation	Variables	Unit
AP	Annual precipitation	m
MAT	Mean annual temperature	°C
SOC	Soil organic carbon stock	kg C m ⁻²
TN	Soil total nitrogen stock	kg N m ⁻²
C/N	Ratio of carbon to nitrogen	None
pH	Soil pH	None
CLA	Soil clay content	%
SAN	Soil sand content	%
STP	Soil total phosphorus	g kg ⁻¹
SAP	Soil available phosphorus	mg kg ⁻¹
SAK	Soil available potassium	mg kg ⁻¹
BD	Soil bulk density	g cm ⁻³
CEC	Cation exchange capacity	cmol kg ⁻¹
FR	Fine root production	kg C m ⁻² yr ⁻¹
LF	Litter fall biomass	kg C m ⁻² yr ⁻¹
R_s	Soil respiration	kg C m ⁻² yr ⁻¹
R_h	Heterotrophic respiration	kg C m ⁻² yr ⁻¹
$R_{0.5\text{ cm}}$	Basal soil respiration at 5 cm	μmol m ⁻² s ⁻¹
$R_{0.10\text{ cm}}$	Basal soil respiration at 10 cm	μmol m ⁻² s ⁻¹
$R_{0.?\text{ cm}}$	Basal soil respiration at other depths	μmol m ⁻² s ⁻¹
$Q_{10.5\text{ cm}}$	Soil (5 cm) temperature sensitivity of soil respiration	None
$Q_{10.10\text{ cm}}$	Soil (10 cm) temperature sensitivity of soil respiration	None
$Q_{10.?\text{ cm}}$	Soil (other depths) temperature sensitivity of soil respiration	None
EL	Elevation	m
TA	Tree age	yr
PD	Plant (tree) density	no. hm ⁻²
DBH	Diameter at breast height	cm
TH	Tree height	m
BA	Basal area of tree	m ² hm ⁻²
LAI	Leaf area index	m ² m ⁻²
ST	Mean annual soil temperature	°C
SM	Mean annual soil moisture	V V ⁻¹

We hypothesized that annual soil temperature (ST) and moisture (SM) data could be fitted with a sinusoid curve, as many sites were located in monsoon climate zones. Moreover, nearly all of the soil temperature and moisture measurements in the literature were evenly spaced. Therefore, we used the digitized maximum and minimum values of ST and SM to generally estimate the annual mean values, although these values are not very accurate

3.2 The relationship between R_0 and Q_{10} in the different ecosystems

The relationship between R_0 and Q_{10} varied among the different ecosystems (Fig. 2a–i). The relationship between R_0 and Q_{10} in the BNMF ($R^2=0.545$, $P<0.001$), DBF ($R^2=0.202$, $P<0.001$), and EBF ($R^2=0.362$, $P<0.001$) ecosystems was explained by a power model (Fig. 2a, c, f). The relationship between R_0 and Q_{10} in the cropland ($R^2=0.701$, $P<0.001$) and grassland and tundra ($R^2=0.387$, $P<0.001$) was explained by an exponential model (Fig. 2b, h). R_0 was also significantly ($P<0.05$) correlated with Q_{10} in the DNF, ENF, and shrubland (Fig. 2d, g, i). Although

the models that simulated the variations in R_0 were different in the different ecosystems, R_0 decreased with the increase in Q_{10} in each ecosystem. As shown in Fig. 2a–i, the R_0 at different depths, particularly at 5 and 10 cm, had similar decreasing patterns with increasing Q_{10} .

3.3 Variables controlling the variations in R_0

A power model based on Q_{10} explained 16.3% ($R^2=0.163$) of the variation in R_0 , with a P value less than 0.001 (Fig. 3a). The relationship between R_0 and FR was explained by a logarithmic model ($R^2=0.245$, $P<0.001$) (Fig. 3b). R_0 was also correlated with LF, soil respiration,

Table 2 Equations for calculating RMSE, ME, MAE, AIC, and BIC. The RMSE, ME, MAE, AIC, and BIC represent the root mean squared error, model efficiency, mean absolute error, Akaike information criterion, and Bayesian information criterion, respectively. Y_{c_MOD} and Y_{c_OBS} are the modelled and observed R_0 or Q_{10} values, respectively; \bar{Y}_{c_OBS} is the mean of $Y_{c_OBS,i}$; n is the sample capacity; SSE is the sum of squares for error; and p is the number of predictors in the model

Statistics	Equations
RMSE	$\sqrt{\frac{\sum_{i=1}^n (Y_{c_MOD,i} - Y_{c_OBS,i})^2}{n}}$
ME	$\frac{[\sum_{i=1}^n (Y_{c_OBS,i} - \bar{Y}_{c_OBS})^2 - \sum_{i=1}^n (Y_{c_MOD,i} - Y_{c_OBS,i})^2]}{[\sum_{i=1}^n (Y_{c_OBS,i} - \bar{Y}_{c_OBS})^2]}$
MAE	$\frac{\sum_{i=1}^n Y_{c_MOD,i} - Y_{c_OBS,i} }{n}$
AIC	$n \ln(SSE) + 2 \times (p + 1) - n \ln(n)$
BIC	$n \ln(SSE) + (p + 1) \times \ln(n) - n \ln(n)$

C/N, and PD, and a nonlinear or linear model including one of these variables explained the variations in R_0 , with a P value less than 0.001 (Fig. 3c–f).

In addition to Q_{10} , FR, LF, soil respiration, C/N, and PD, a heatmap of Pearson’s correlation indicated that R_0 was significantly ($P < 0.05$) correlated with other variables (i.e., SOC, heterotrophic respiration, and DBH) (Fig. 3g). Q_{10} was significantly ($P < 0.05$) correlated with climate (i.e., AP and MAT), soil (i.e., SOC, TN, and BD), and vegetation (i.e., LF, PD, TH, BA, and LAI) factors and soil temperature and moisture. It was obvious that two variables (i.e., LF and heterotrophic respiration) were positively and significantly ($P < 0.05$) correlated with R_0 but were negatively and significantly ($P < 0.05$) correlated with Q_{10} . A number of variables in Fig. 3g were significantly ($P < 0.05$) correlated with each other. Therefore, not all potential controlling factors could be used to establish the R_0 and Q_{10} models. Our dataset also reflects a high variability in the controlling factors for R_0 and Q_{10} . Moreover, the driving factors of soil respiration differed in the different ecosystems (Table S2). AP and MAT were key factors controlling the variations in soil respiration in most ecosystems. Soil respiration was significantly ($P < 0.05$) correlated with soil factors (i.e., SOC, TN, and C/N) and FR rather than AP and/or MAT in the DBF. Soil respiration was significantly ($P < 0.05$) correlated with soil factors (e.g., SOC, TN, and C/N) in most ecosystems and was significantly ($P < 0.05$) correlated with vegetation factors (e.g., FR, TA, DBH, and BA) in the cropland, DBF, DNF, EBF, and grassland and tundra ecosystems.

A model [Eq. (3)] that included Q_{10} , FR, and C/N explained 75.0% ($R^2 = 0.750$, $P < 0.001$) of the variation in R_0 :

$$R_0 = 1.215e^{-0.549Q_{10}+0.804FR+0.043C/N} \quad (3)$$

$$(R^2 = 0.750, n = 58, P < 0.001)$$

A model expressed as Eq. (4) further explained 66.3% ($R^2 = 0.663$, $P < 0.001$) of the variation in Q_{10} . This model in which the key controlling factors (i.e., AP, MAT, TN, BD, and LAI) were included satisfactorily simulated Q_{10} across all ecosystems.

$$Q_{10} = 4.444e^{0.437AP-0.044MAT+0.348-0.609BD+0.006LAI} \quad (4)$$

$$(R^2 = 0.663, n = 58, P < 0.001)$$

Figure 4a indicates that the relationship between the observed and modelled R_0 was well fitted with a linear regression function and the slope of the regression line was very close to the 1:1 line. The RMSE, ME, MAE, AIC, and BIC for Eq. (3) were 0.338, 0.750, 0.503, -117.676, and -109.435, respectively. The relationship between the observed and modelled Q_{10} was also well fitted with a linear regression function, with a slope of the regression line very close to the 1:1 line (Fig. 4b). The RMSE, ME, MAE, AIC, and BIC for Eq. (4) were 0.545, 0.663, 0.667, -58.511, and -46.148, respectively. Structural equation modelling indicated that FR and C/N were more important in predicting the variations in R_0 than Q_{10} (Fig. 5a). When the comprehensive effects of the three controlling factors on R_0 in the structural equation modelling were considered, the effect of Q_{10} was negative, but the effects of FR and C/N were positive. Structural equation modelling showed that TN and BD were more important in predicting the variations in Q_{10} than climate factors (i.e., AP and MAT) (Fig. 5b). The effect of LAI was also more important than that of AP.

4 Discussion

4.1 Relationship between R_0 and Q_{10} in the different ecosystems

We analyzed the R_0 and Q_{10} values of soil respiration based on the soil temperature at 5 cm, 10 cm and other depths, which are widely used to measure soil respiration and establish soil respiration models (Hursh et al. 2017; Jian et al. 2021; Stell et al. 2021). Our study showed wide variability in R_0 in most ecosystems. The soils with poor nutrient conditions in the desert exhibited low R_0 , indicating competing C accessibility. Meanwhile, deserts usually appear in warm regions (i.e., temperate, subtropical and tropical zones), which may decrease Q_{10} .

Our analyses provide evidence for the “C quality-temperature” hypothesis, which indicates that the CO_2 emissions of low-quality substrates have a higher Q_{10} than the CO_2 emissions of more labile substrates (Fierer

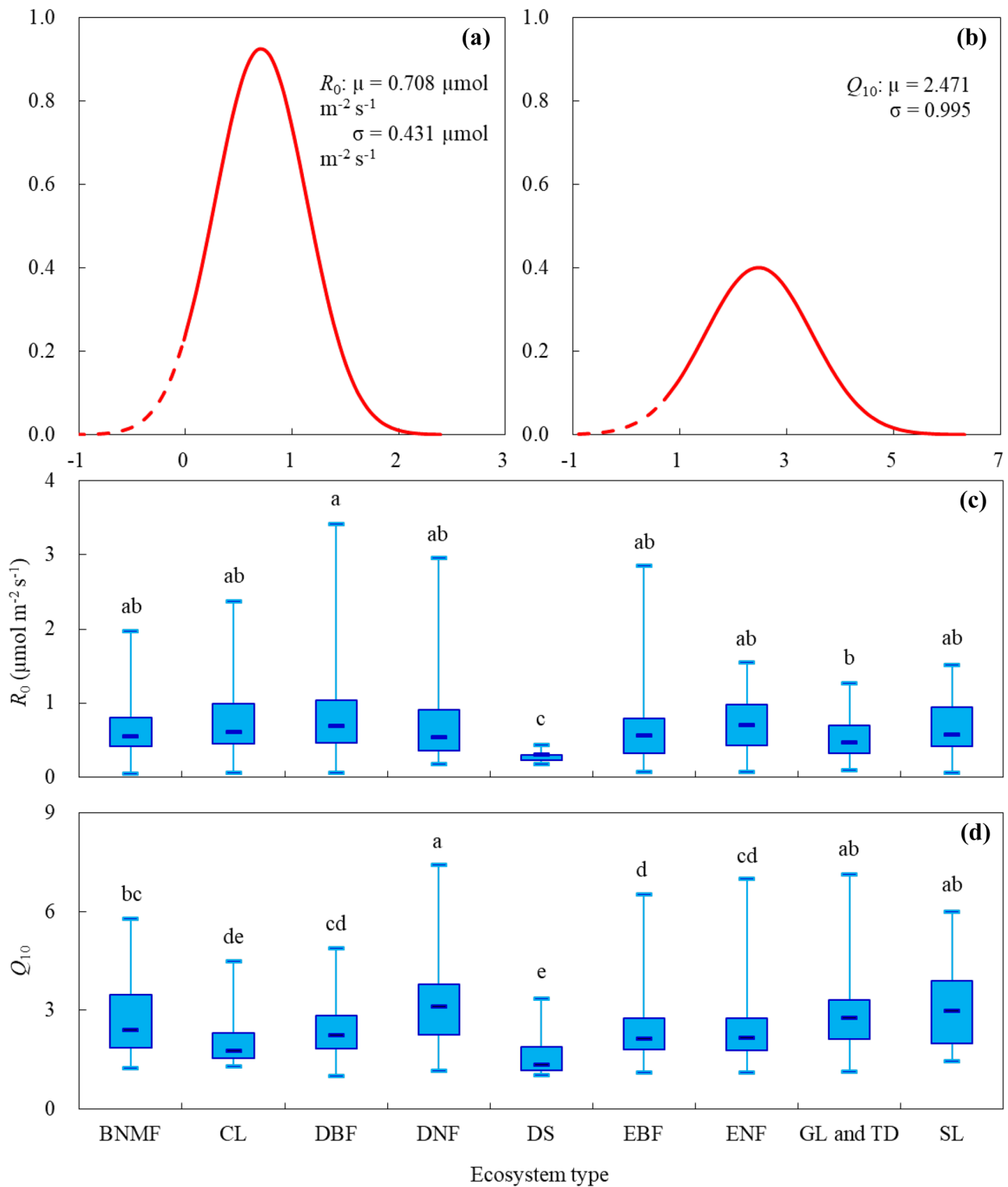


Fig. 1 The distribution patterns of R_0 **a** and Q_{10} . **a, b** Normal distribution curves for R_0 and Q_{10} , respectively, across the different soil depths (5 cm, 10 cm, and other depths) and the different ecosystems. **c, d** Box-and-whisker plots for R_0 and Q_{10} , respectively, across the different soil depths (5 cm, 10 cm and other depths). BNMF, CL,

DBF, DNF, DS, EBF, ENF, GL and TD, and SL represent broad-leaf and needle-leaf mixed forest, cropland, deciduous broad-leaf forest, deciduous needle-leaf forest, desert, evergreen broad-leaf forest, evergreen needle-leaf forest, grassland and tundra, and shrubland, respectively

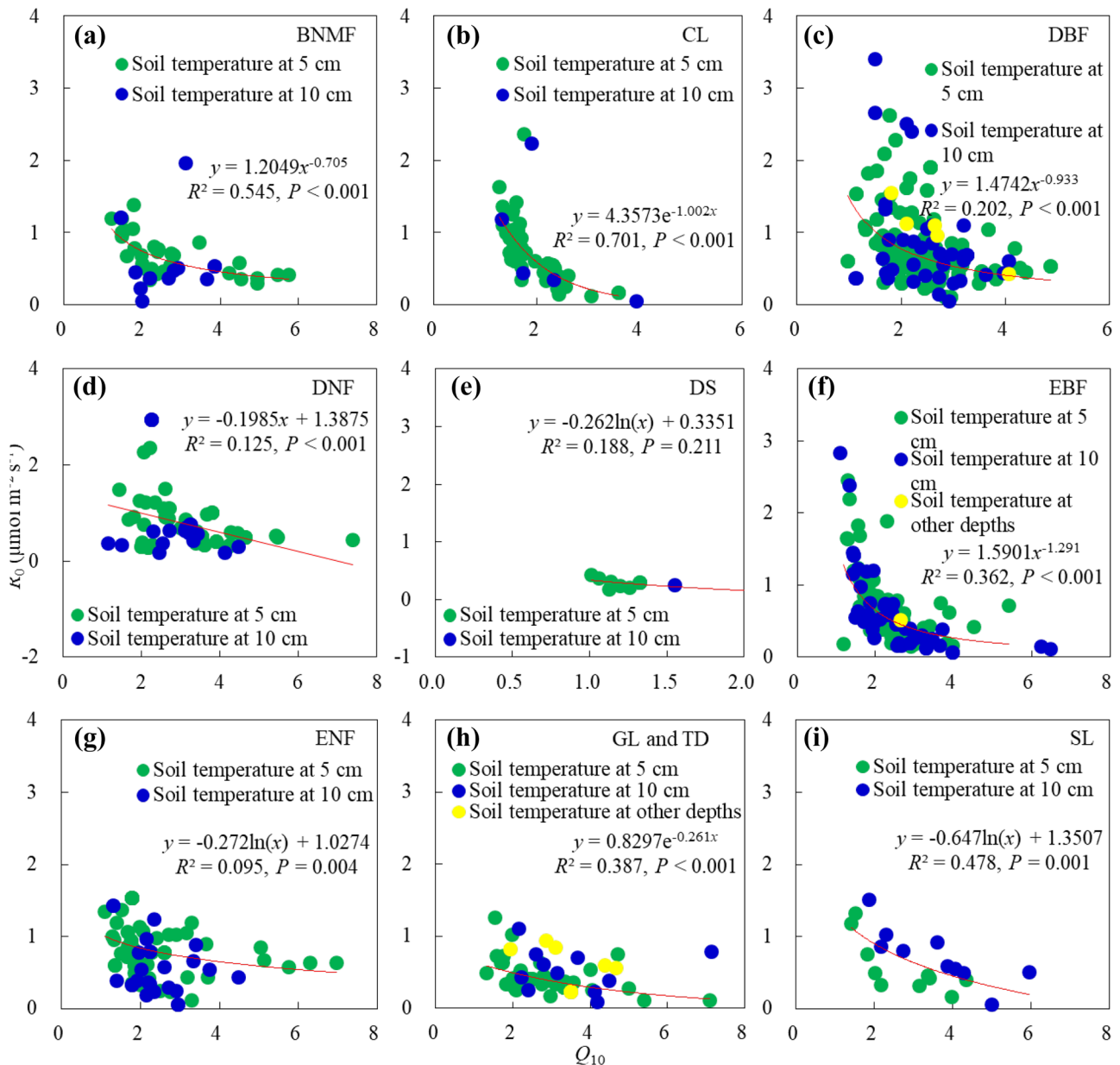


Fig. 2 Relationship between R_0 and Q_{10} in the different ecosystems. **a–i** BNMF, CL, DBF, DNF, DS, EBF, ENF, GL and TD, and SL, respectively. BNMF, CL, DBF, DNF, DS, EBF, ENF, GL and TD, and SL represent broad-leaf and needle-leaf mixed forest, cropland,

deciduous broad-leaf forest, deciduous needle-leaf forest, desert, evergreen broad-leaf forest, evergreen needle-leaf forest, grassland and tundra, and shrubland, respectively

et al. 2006). Previous field studies have shown an inverse relationship between C quality and Q_{10} (Knorr et al. 2005; Fierer et al. 2006; Luan et al. 2018). A process-based model has predicted the relationship between C quality and Q_{10} (Liski et al. 1999), and a long-term soil experiment involving incubation and land conversion studies also supports the “C quality-temperature” theory (Giardina and Ryan 2000). Karhu et al. (2010) found that older soil C had a lower R_0 than younger C from root exudates and plant litter. A higher Q_{10} value of CO_2 emissions

in the humus layer than in the litter layer was reported for a *Pinus resinosa* plantation, which may be attributed to the fact that the humus layer has more recalcitrant forms of C (Malcolm et al. 2009).

The models based on Q_{10} explaining the variations in R_0 had different R^2 values that varied from 0.095 to 0.701 (Fig. 2a–i), indicating the complexity of the relationship between R_0 and Q_{10} in various ecosystems. For instance, cropland exhibited an obvious decreasing pattern of R_0 with the increase in Q_{10} . Vegetation influences soil C accessibility

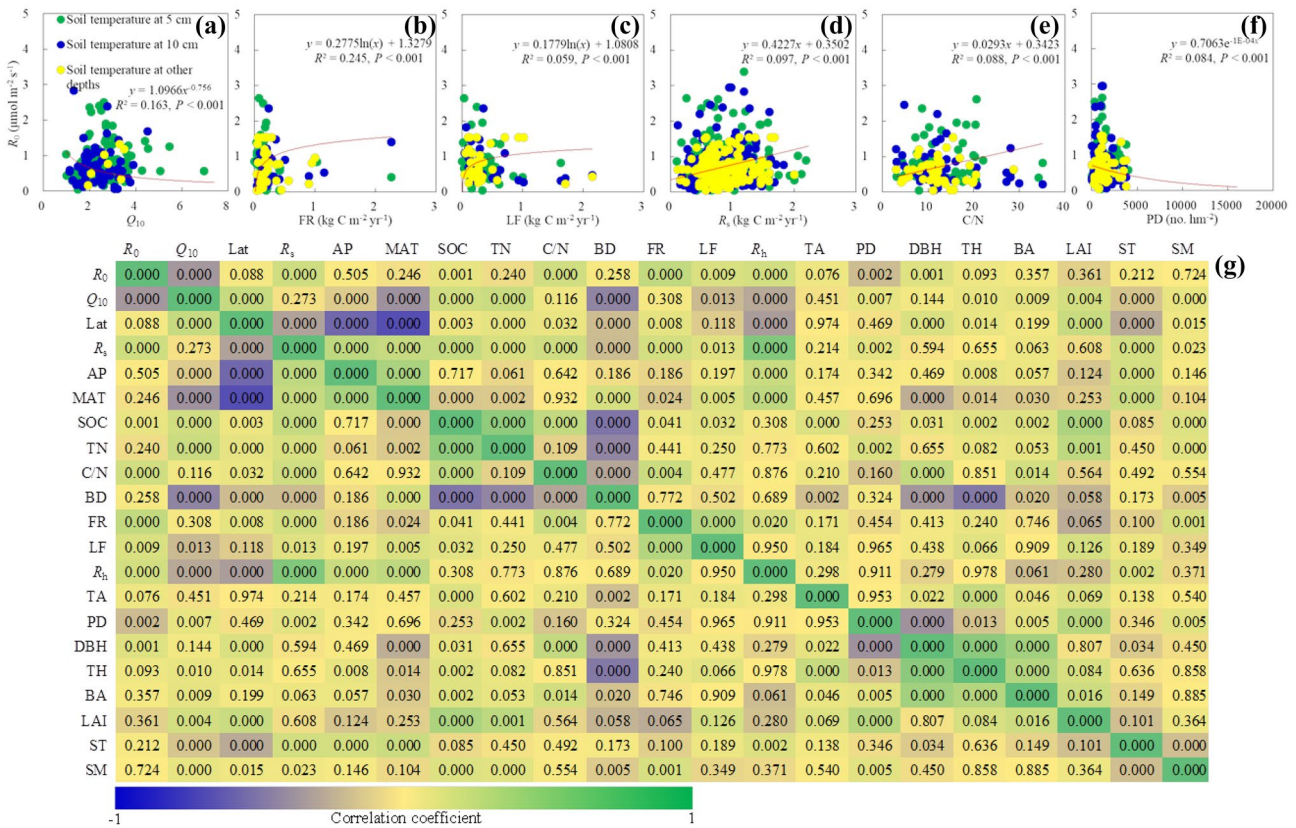


Fig. 3 Relationships between R_0 and Q_{10} across the different soil depths (5 cm, 10 cm and other depths) and the different ecosystems and a heatmap of Pearson's correlations between the variables R_0 , Q_{10} , latitude (Lat), R_s , AP, MAT, SOC, TN, C/N, BD, FR, R_h , TA, PD, DBH, TH, BA, LAI, ST, and SM (abbreviations as indicated in

Table 1). **a–f** Explanatory variables Q_{10} , FR, LF, R_s , C/N, and PD, respectively. **g** Heatmap of Pearson's correlations. The colors in **g** reveal the correlation coefficients, and the numbers in the boxes are P values

through above- and belowground litter inputs and root exudates (Hereş et al. 2021; Mujica et al. 2021). Different ecosystems differ in vegetation characteristics, such as FR and LF, resulting in different amounts and components of C inputs from plants to soils, which may influence microbial activity and C quality (R_0) (Bradford et al. 2019; Fierer et al. 2005).

4.2 Modelling R_0 using climate, soil, and vegetation factors

Figure 3a–f indicate the potential effects of Q_{10} , FR, LF, soil respiration, C/N, and PD on R_0 . There were two main seasons in which these factors were potentially influencing factors related to R_0 . First, R_0 has been suggested to be negatively correlated with Q_{10} according to the “C quality–temperature” theory (Bosatta and Ågren 1999; Fierer et al. 2006; Hashimoto 2005). Soil respiration determines the magnitude of R_0 across different ecosystems (Phillips et al. 2016). Second, FR, LF, and PD are vegetation characteristics that reveal the amount of substrates that are provided by vegetation to basal soil respiration (Dusza

et al. 2020; Shi et al. 2019). The soil factor C/N is related to the quality of substrates for basal soil respiration (Davidson and Janssens 2006; Malek et al. 2021). The model based on Q_{10} , FR, and C/N to simulate R_0 suggested that the variations in R_0 across different ecosystems were controlled by a combination of Q_{10} and other vegetation and soil factors. Here, FR, rather than LF and PD, was included in the R_0 model because FR was a more direct variable that was related to belowground basal soil respiration and had a greater correlation coefficient than LF and PD (Fig. 3b, c, f). C/N was chosen in the model because it was highly significantly correlated with R_0 (Fig. 3e, g). FR and C/N interacted with Q_{10} and drove the variations in R_0 , while soil (i.e., TN and BD) and vegetation (i.e., LAI) factors interacted with precipitation and temperature when Q_{10} was modelled. Only a small part (25.0%) of R_0 was controlled by variables other than Q_{10} , FR, and C/N. Similar to R_0 , only 33.7% ($R^2=0.337$) of the variation in Q_{10} was controlled by variables other than AP, MAT, TN, BD, and LAI. The relationship between Q_{10} and temperature contributes to uncertainty in predicting the response of the terrestrial SOC pool to future climate warming. A significant negative correlation between

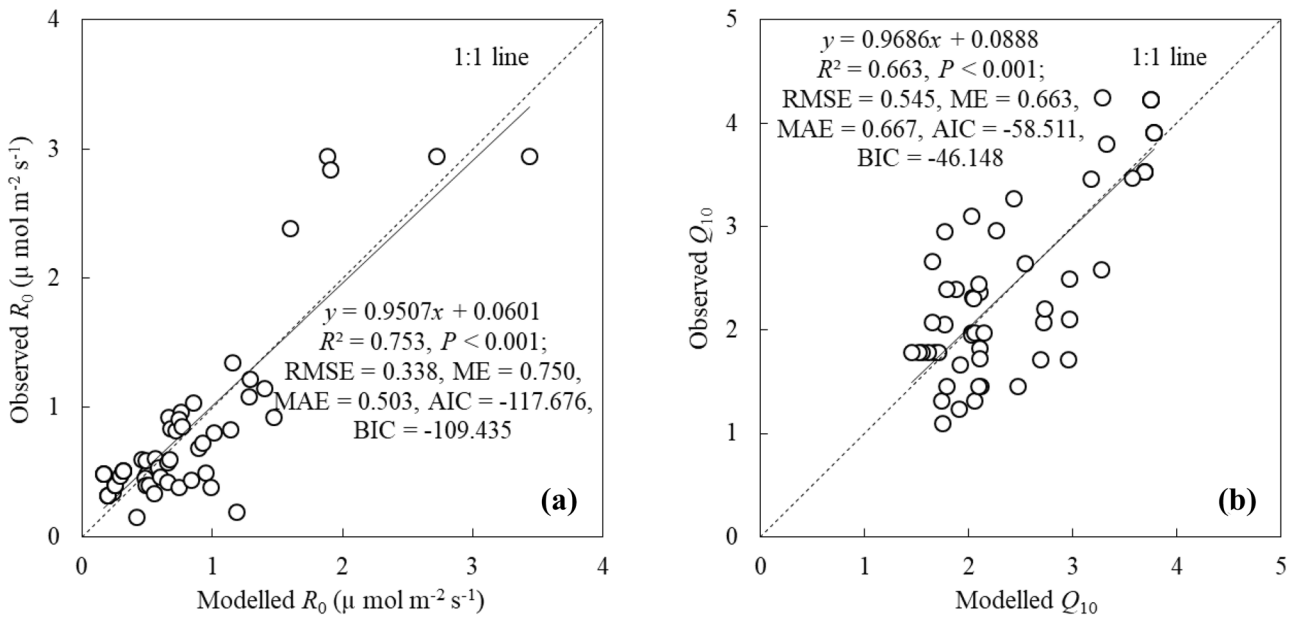


Fig. 4 Relationship between the observed and modelled R_0 and that between the observed and modelled Q_{10} . **a, b** R_0 and Q_{10} , respectively. RMSE, ME, MAE, AIC, and BIC represent root mean squared

error, model efficiency, mean absolute error, Akaike information criterion, and Bayesian information criterion, respectively

Q_{10} and MAT has been reported by several previous studies, suggesting that the increase rates of soil respiration with the increase in temperature may decrease under a warmer environment (Hursh et al. 2017; Peng et al. 2009; Rustad et al. 2001; Zheng et al. 2009). Similar to what was shown in our study, Feng et al. (2018) found correlations between Q_{10} in grassland and AP and between Q_{10} and aboveground biomass, which is

related to LAI (Ribeiro et al. 2008). Moreover, the correlations between Q_{10} and TN and BD indicated that soil nutrients and physical properties regulated the responses of soil respiration to temperature (Davidson and Janssens 2006; Yu et al. 2017). As shown in the Q_{10} model, soils with rich TN and low BD may facilitate the improvement of soil microbial activity and may thus result in a higher Q_{10} . Q_{10} has been considered a constant

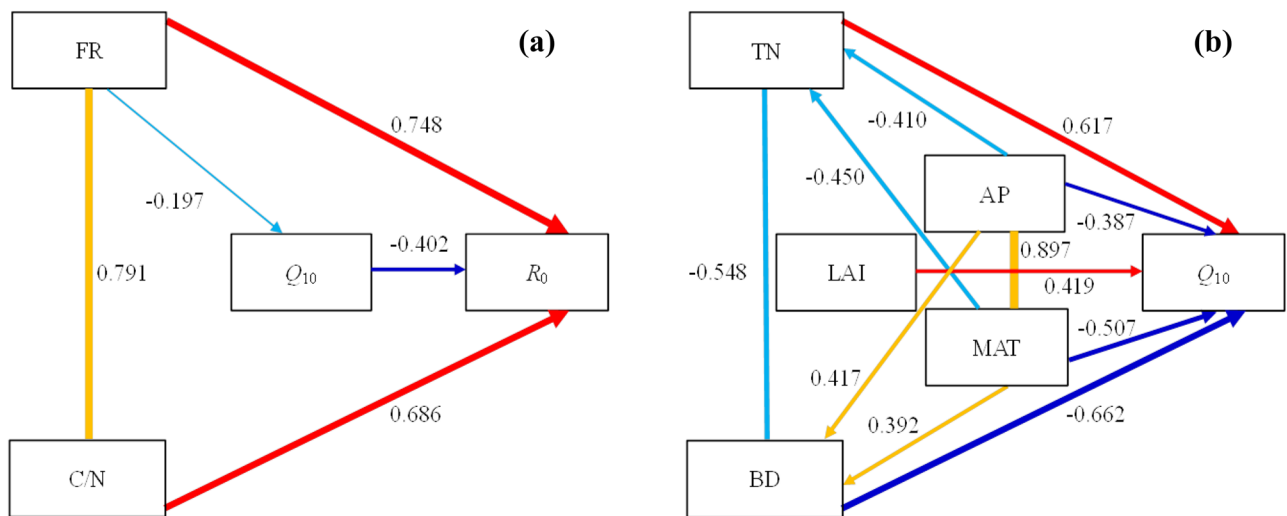


Fig. 5 Structural equation modelling of R_0 and Q_{10} . **a, b** R_0 and Q_{10} , respectively. The correlations among variables based on the covariance matrix are indicated in the structural equation modelling. The variables used for modelling R_0 across the different soil depths (5 cm,

10 cm, and other depths) and the different ecosystems were Q_{10} , FR, and C/N (abbreviations as indicated in Table 1). The variables used for modelling Q_{10} were AP, MAT, TN, BD, and LAI

with a value of 2 in most terrestrial models (Jenkinson et al. 1991; Lenton and Huntingford 2003; Schimel et al. 2000). Our study showed the great variability in Q_{10} and modelled Q_{10} using AP, MAT, TN, BD, and LAI. The Q_{10} model included more variables and had a higher R^2 than the models in previous studies (Peng et al. 2009; Zheng et al. 2009), which provided a basis for simulating the seasonal variations in soil respiration.

Table S1 also reflects a high variability in the controlling factors of R_0 and Q_{10} . Although not all data that we collected in this study were obtained through absolutely identical approaches and minimized the existing errors, the measurements of a key variable soil respiration in the different sites used common and comparable methods (Bekku et al. 1997; Wang and Wang 2003). However, random errors for measuring some soil and vegetation factors in the different sites may exist. Most researchers do not point out the detailed measurement methods to determine soil and vegetation factors, as they are shown as background site information. It is difficult to obtain identically measured soil and vegetation factors based on the available data. Therefore, the existing errors in measuring soil and vegetation factors may partly contribute to the modelling uncertainty, which reduce the performance of the R_0 and Q_{10} models.

Soil- and vegetation-associated variables are influenced by climate factors, particularly in climatic extremes (e.g., tropical and frigid zones), which strongly control the variations in Q_{10} . This phenomenon is related to the lack of mineral stabilization of C in cold zones, resulting in a faster response of microorganisms to increasing temperature (Haaf et al. 2021). The decomposition rates of soil C were related to the temperature sensitivity of soil respiration, with a recalcitrant C quality when Q_{10} was relatively high under cold conditions. Soil C decomposes faster in cold climates once temperature barriers are released during the warming process compared with warm climates (Bradford 2013; Melillo et al. 2017).

Q_{10} is not a separate dominant controlling factor of R_0 , and climate factors have little impact on Q_{10} under moderate climate conditions (Phillips et al. 2016). A wide range of soil properties controlled the variations in R_0 across all of the ecosystems, leading to high heterogeneity. Our study allowed us to predict the temporal and spatial variations in R_0 using Q_{10} and vegetation and soil factors, and Q_{10} could further be expressed as a function of climate, soil, and vegetation variables. The relatively high R^2 value in the multiple regression models indicated that the interactions between R_0 and Q_{10} and other predictors were reliable. The models for R_0 could be further used to explain the potential of different percentages of labile and recalcitrant C components in soils of different ecosystems to emit CO_2 . The variability in R_0 that was not explained by the vegetation and soil factors in this study may be partly due to the nutrient limitation strategies in some ecosystems (e.g., desert), which reduced the

effects of other factors, such as temperature, on microbial and root respiration (Monson et al. 2006; Stone et al. 2021).

Low temperature inhibits C mineralization under cold climate conditions, which may reduce soil activity. In cold climates, tree residues (e.g., stems, litter and roots) that are usually not mineralized are the main substrates and energy for microorganisms (Doetterl et al. 2015; Kramer and Chadwick 2018). Soils in warmer climates have higher chemical reactivity and stabilization potential for C and respond less to increasing temperature than those in cold climates (Meyer et al. 2018). The largest range of R_0 in the DBF may be attributed to the diversity of C sources and C-associated energy (Cusack et al. 2018; Kramer and Chadwick 2018). Specifically, the crop residues in the cropland in the warm climates are often composed of more similar C components during the mineralization process than the tree residues in the cold climates, resulting in the strong correlation between R_0 and Q_{10} in the cropland compared with that in the DBF and DNF ecosystems (Fig. 2b, c, d). The R_0 that varied substantially in the DBF may be partly due to the diversity of soil C stabilization controlled by the vegetation-associated soil development status (Bahn et al. 2010; Čater et al. 2020; Nghalipo and Throop 2021). The modelling of R_0 provided the basis for modelling the temporal variations in soil respiration at the seasonal scale when the R_0 model was coupled with the Q_{10} model, although the data points of predictors in the models that were simultaneously measured are still lacking and need to be increased in the future.

Q_{10} was a key variable to predict R_0 in this study, and the effects of Q_{10} on R_0 interacted with other controlling factors. It has been widely reported that Q_{10} varies considerably in different ecosystems (Davidson et al. 2006; Morote et al. 2021). We determined the variations and driving factors of Q_{10} and used this key variable to further simulate the variations of R_0 . The effects of climate, soil, or vegetation factors on Q_{10} have been found in previous studies (Gutierrez-Giron et al. 2015; Rodtassana et al. 2021; Wang et al. 2010, 2016). We also found comprehensive effects of these factors on Q_{10} . The Q_{10} model including climate, soil, and vegetation factors provided a prerequisite to quantify the variations in R_0 , which made R_0 predictable by using climate, soil, and vegetation factors.

5 Conclusions

Our study showed great variability in R_0 and Q_{10} among the different ecosystems. Our study confirmed the negative correlations between R_0 and Q_{10} in the different ecosystems, but the best fitting models that explained the relationship between R_0 and Q_{10} differed among these ecosystems. The fitting performance of the model to simulate R_0 based on Q_{10} was better in the cropland than in the DNF and DBF ecosystems, indicating the difference in soil C sources derived

from crop and tree residues. A model that included Q_{10} , FR, and C/N explained 75.0% ($R^2 = 0.750$) of the variation in R_0 , and Q_{10} could further be expressed as a model ($R^2 = 0.663$) based on AP, MAT, TN, BD, and LAI. This study provides reliable models to explain the spatial and temporal variations in R_0 , which can potentially be used to improve terrestrial C cycle models by considering the comprehensive effects of Q_{10} and soil and vegetation factors.

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Availability of data and material All data generated or analyzed during this study are included in this published article and its supplementary materials.

Code availability Not applicable.

Declarations

Ethics approval This study does not involve animals.

Consent to participate This study does not involve human participants.

Conflict of interest The authors declare no competing interests.

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